BIOLOGY AND POPULATION DYNAMICS OF THE KING MACKEREL (*Scomberomorus commerson*, Lacepède, 1800) OFF THE COAST OF NATAL

by

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PREFACE

The work described in this thesis was carried out whilst based at the Oceanographic Research Institute, Durban and under the supervision of Professor A.J. de Freitas (Director) and Mr R.P. van der Elst (deputy director).

This study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work or research samples of others it has been duly acknowledged in the text.

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ABSTRACT

This thesis provides a study on aspects of the biology and population dynamics of *Scomberomorus commerson* off the south east coast of southern Africa. This is necessary for the evaluation of the current management policies and for the selection of the "best" management strategy for this species off the coast of Natal. The current status of *S. commerson* off the Natal coast was assessed in terms of yield-per-recruit and spawning biomass-per-recruit analyses. Input parameters to these per-recruit models include growth and mortality rates and basic biological data. Estimates of these parameters and the methods employed are detailed in the thesis.

S. commerson has a protracted spawning period ranging from November to March. The principal spawning area is Mozambique. Fifty percent sexual maturity is attained at 1096mm and 706mm(FL) for females and males, respectively. The ratio of males to females in the sampled catches is approximately 1:2 with females attaining a significantly larger mean size: females (926mm,FL) and males (898mm, FL). The mass-length relationship for both sexes can be described by the following equation:

$$Mass(g) = 0.1353x10^{-5}.[FL(mm)]^{3.2515}$$

Growth parameter estimates for the combined sexes were estimated from a length-based as well as an age-based method. An objective technique was utilised to determine which growth function best describes the age-length data of *S. commerson*. Age data were obtained from otolith readings. The precision of otolith readings was described by an index. This index, the average percent error, which is equal to 20.25%, is higher than that recorded in other studies. Two opaque bands are laid

down annually. This was validated by marginal increment analyses as well as from tagging data. The age-length relationship, assuming biannual periodicity of the opaque band, is best described by a Von Bertalanffy growth function:

$$L_{\text{age}}\ (mm, FL) = 1344mm\left(1-e^{-0.292\ \text{yr}^{-1}(\text{age}+2.999\ \text{yrs})}\right)$$

The instantaneous natural mortality rate (M) was estimated using two different techniques: the Pauly equation and the Rihkter and Efanov equation. The former equation was very sensitive to changes in the mean environmental temperature and both techniques produced different estimates. The average of both methods was, therefore, taken as an estimate of M which is 0.5 yr^{-1}. The instantaneous fishing mortality rate (F) is currently estimated to be 0.25 yr^{-1}. This estimate is, however, positively biased as the effects of emigration have not been taken into account.

The per-recruit analyses were conducted for three different growth equations for the same values of F and M, age-at-maturity and age-at-first-capture. For all growth equations the yield-per-recruit increased with increased fishing with maximum yield-per-recruit attained either at infinite F or at very high values of F ($> 5\ \text{yr}^{-1}$). $F_{0.1}$ was attained between 0.6 and 0.8 yr^{-1} for all growth equations. The Von Bertalanffy growth function, assuming annual periodicity of the opaque band, was the most unrealistic. It predicted a virtual collapse of the fishery when F=M and a reduction of the spawning biomass to 50% of its unfished level at F=0.1 yr^{-1}. The length based derived growth equation and the Von Bertalanffy growth function, assuming biannual periodicity of the opaque band, predicted that spawning biomass dropped to 50% of the pristine level at F=0.19 and 0.16 yr^{-1}, respectively. It is believed that the current restrictions on sport catches of 10 fish/person/day offers adequate protection for the

Natal king mackerel stock. These restrictions should be maintained in Natal. However, if fishing effort on this species continues to increase (as is anticipated in an open access fishery) or if there is increased commercial interest or if there is renewed fishing in Mozambique, a minimum size is recommended to adequately protect the spawning stock. Such a minimum size should be implemented in Mozambique which is the principal spawning area for king mackerel. Setting a minimum size in Natal, above the size-at-50% maturity may substantially reduce catches in the short and medium term because at least 90% of the catch currently taken will be inaccessible to fishermen. Restrictions of king mackerel catches in Natal, alone, is not considered a viable management option as Natal's commercial and to a certain extent recreational fishermen may turn to Mozambican waters to harvest king mackerel. Management options should be implemented and enforced both in Natal and Mozambique.

CONTENTS

INTRODUCTION

The most important gamefish to recreational and commercial skiboat fishermen off the Natal coast is the king mackerel *Scomberomorus commerson* (van der Elst and Collette, 1984). It belongs to the family Scombridae which includes the mackerels, bonitos and tunas (Collette and Nauen, 1983). It is an epipelagic fish widely distributed in the warm waters of the Red Sea and Indo-Pacific regions (Smith and Heemstra, 1986). On the east coast of southern Africa it ranges from Mossel Bay, to Transkei, to Natal and northwards into Mozambique (van der Elst, 1988). It occurs in slightly deeper waters over the continental shelf of Natal (Smith and Heemstra, 1986) but does occur close to shores (van der Elst, 1988). Although the most common size taken is 900mm(FL), it can attain at least 2200mm(FL) (Collette and Nauen, 1983). The all-tackle angling record is a 44.9kg fish taken off Scottburgh, Natal (Collette and Nauen, 1983). Off Natal, recreational and commercial skiboat anglers catch king mackerel by trolling lures or dead bait such as pilchards or live bait using rod and line (van der Elst, 1988; van der Elst and Collette, 1984). *S. commerson* is also actively pursued by spearfishermen. Natal's commercial and recreational fishery is a multi-species, multi-user fishery. In 1989, 68% of the catch by number (comprising of 94 species), that were taken by sport anglers, consisted of *S. commerson*. During this same period this species made up 53% of the catch by number of spearfishermen. According to the National Marine Linefish Catch Statistics Programme 12% by weight of the total commercial catch off Natal and Transkei in 1989 consisted of *S. commerson*.

In the current South African linefish legislation *S.commerson* is classified as an exploitable species with commercial and semi-commercial fishermen having no restrictions on mass or numbers harvested, however, recreational anglers and spearfishermen are limited to 10 fish (in the exploitable class)/person/day. This implies that, theoretically, the maximum catch of *S. commerson* per sport angler per day is 10. At present there is no minimum size restriction for either sport or commercial fishermen. However, at a recent symposium on marine recreational fishing Natal anglers have identified a need for a minimum size limit for *S. commerson* (Winch, 1990).

Previously little was known of the biology and population dynamics of *S. commerson* in southern Africa. This study, therefore, addresses some of these aspects in order to assess the current status of this fishery and to develop a management strategy which will ensure sustained future catches of king mackerel.

STUDY AREA AND GENERAL SAMPLING METHODS

Sampling was undertaken on an irregular basis over a nineteen year period from 1972 to 1991 and was undertaken mainly by Mr Rudy van der Elst of the Oceanographic Research Institute, Durban. Samples were obtained from both recreational and commercial catches from the following areas: Natal, Zululand and Mozambique. Sampling in Mozambique was limited. Sampling was mainly confined to angling and spearfishing tournaments. Sampling methods in this study conform to the standard techniques adopted by the Oceanographic Research Institute, Durban in its teleost study. In the field or in the laboratory the following were recorded:

1. Date and locality of capture.
2. The linear fork length of the fish, from the tip of the snout to the fork of the tail, was measured to the nearest 0.5cm. Total length from the tip of the snout to the upper caudal lobe rotated to the midline was also measured. For small specimens the lengths were recorded to the nearest millimetre.
3. The sex was determined whenever possible and the gonad maturity stage was macroscopically assessed (Chapter 1).
4. Total body mass was measured by a spring balance to the nearest 0.1g for very small specimens; intermediate sized specimens were measured to the nearest 1g while large specimens were measured to the nearest 0.1kg. Gonad mass to the nearest 0.1g was also recorded, whenever possible. In some cases, only the head region of the fish was made available. In these instances otoliths were removed for age determination and the maxillary length (from the tip to the most posterior part of the upper jaw) was measured using vernier calipers to the nearest 0.01mm. The maxillary length provided an estimate of the length of the fish.
5. Otoliths were removed whenever possible. These where washed in tap water to remove the saccular membranes and then stored dry in gelatin capsules to prevent breakage. One month prior to age determination the otoliths were stored in glycerin. It was found from previous trials that glycerin cleared the otoliths which improved the readings of the banding. For age readings, otoliths were immersed in ethanol and read against a black background, under a dissecting microscope using reflected light.

Readings were conducted with no prior knowledge of fish length, date or locality of capture.

Samples less than 400mm were obtained by research sampling and from prawn trawler bycatches off Mozambique. Sampling during certain months was often limited because king mackerel was either not abundant during these months (due to the coastal migratory nature of this species) or that weather conditions during these months prevented the launching of skiboats. In the field, removal of otoliths for age determination was very time consuming and difficult. It takes approximately 15 to 20mins to remove the pair of sagittae otoliths (without breaking them), to record the length, mass and sex for each fish. Because it was time consuming heads were removed for processing in the laboratory. In these instances, to allow for speedier handling of the fishermen's catch (who were sometimes reluctant for their catch to be handled) the sex and fish length were not recorded. As a result only a limited database of age-length data for the seperate sexes was collected and hence no sex specific growth curves could be fitted.

CHAPTER ONE

1. REPRODUCTIVE SEASONALITY, SPAWNING AREAS AND MATURITY ASSESSMENT

1.1 Introduction

The management options of closed seasons and minimum size limits, imposed by the current South African fisheries legislation, is usually based on a knowledge of the reproductive seasons and lengths-at-maturity of protected species. A closed season or area reduces effort in the fishery while protecting the resource during a vulnerable portion of its life history eg. during the breeding season fish aggregate and may be easier to capture. A minimum size limit is based on the rationale that a fish should be allowed to spawn prior to being exploited and thereby contribute to future stocks (Buxton, 1990). Basic to this approach to fisheries management are, therefore, knowledge of the breeding season(s), areas of spawning and length-at-50%-maturity.

Many South African fisheries scientists have used the gonadosomatic index (GSI) to determine or confirm the breeding season of various species (Griffiths, 1988; Buxton, 1987; Garratt, 1984; van der Elst, 1976). The GSI is usually the ratio of gonad mass to body size expressed as a percentage (McQuin, 1989) with body size being total mass, somatic mass or the isometric equivalent of total mass (length^3). Assessing the maturity state based on the GSI assumes that as the gonads mature there is a corresponding increase in the size and number of the gametes and hence an increase in gonad mass (deVlaming *et al.*1982). A basic assumption when calculating the GSI is that the linear relationship between gonad mass and body size is constant for different maturity stages (McQuin, 1989). If this relationship is not constant then the GSI is inappropriate to classify maturity stages (deVlaming *et al.*1982). This assumption was tested using data collected for *S. commerson*.

1.2 Materials and methods

The reproductive seasonality of *S. commerson* was investigated by an index of gonad maturation based on a macroscopic staging key. The maturity stages are based on keys described by van der Elst (1976) and Garratt (1984) and modified for this species. The maturity stages are as follows:

FEMALES	MALES
STAGE 1 - IMMATURE The ovary is translucent, orange in colour and extends only about half the length of the body cavity. No ova are visible to the naked eye.	Testis is bilaterally flattened, off- white in colour and extends along half the length of the body cavity. No milt is extrusable.
STAGE 2 - ACTIVE The ovary is yellow-orange in colour. There is an	Testis is off-white and blood supply has increased. Milt is visible in cross-section.

increase in the ovarian blood vessels, the ovarian wall is thickened and ova are visible to the naked eye.	
STAGE 3 - ACTIVE/RIPE Ova are visible within an enlarged yellow ovary. Vascular supply has increased and the ova are closely packed within a transparent ovarian membrane.	Testis is off-white, extends nearly full body cavity length, blood supply is further increased. Creamy milt visible in cross-section. This stage is not easily distinguishable from the ripe stage.
STAGE 4 - RIPE Ovary is very enlarged and is yellow-pink in colour. Vascular supply has substantially increased and the larger ova are tightly packed within a transparent membrane.	Testis is white, extends full body cavity length, is firm to the touch and blood vessels are larger. Milt does not flow freely.
STAGE 5 - RIPE RUNNING Ova are loosely suspended and the slightest pressure can rupture the ovarian membrane and ova flow freely from the cloaca.	Testis is large and firm, milt flows freely at the slightest pressure.
STAGE 6 - PARTIALLY SPAWNED Ovary	Testis off-white and slightly flaccid. Milt is

is yellow-red in colour and haemorrhaging is evident. Opaque ova are evident in the large lumen.	extrusable. Haemorrhaging is evident.
STAGE 7 - SPENT Ovarian membrane is opaque and the ovary is wine-red in colour. The ovary still contains a few ova.	Testis extends full body cavity length, but is much smaller in size, is brown and pink from haemorrhaging. Small amount of milt remains.
STAGE 8 - RESTING MATURE The ovary extends the full length of the body cavity. Ovarian membrane is opaque and no ova are visible to the naked eye. This is an inactive mature stage that reverts to the active stage at the onset of the next spawning season.	Testis extends full body cavity length. No milt is visible. This is an inactive mature stage that reverts to the active stage at the onset of the next spawning stage.

Data for the macroscopic staging of maturity for *S. commerson* were obtained during the period 1972-1991 from recreational and commercial catches made along the Natal, Zululand and Mozambique coasts (n=1741). Only a few specimens were obtained from Mozambique (n=140). To determine the spawning area the frequency of stage 5 (ripe running) in relation to the number of mature females sampled in each region was examined in the following areas - Mozambique, Zululand and Natal. This division of the king mackerel resource into three areas is arbitrary and is based on the assumption that each "stock" will/may be treated separately for management purposes. It does not imply that these "stocks" are genetically isolated.

To assess whether the relationship between ovary mass and body size (somatic mass, fork length) was constant in different stages of ovarian development, an analysis of covariance (McQuin, 1989; deVlaming *et al.* 1982) was used to test for regression parallelism in the different stages (Zar, 1974). Maturity stages 6 and 7 are characterised, respectively, by the shedding of eggs and the reconstructive phase which includes the resorption of unshed eggs. Since these stages do not represent increasing gamete development as measured by stages 8 and 2 to 5, stages 6 and 7 were excluded from the analysis (McQuin, 1989). Only data from mature females were used in the analysis.

In order to determine the length-at-maturity only data obtained during the months of peak reproductive activity, as determined from macroscopic gonad staging, can be used. As stages 1 and 2 represented immature fish and further that stage 8 may have included immature fish (see discussion below), only stages 3 to 7 were used in this analysis (Garratt, 1984; Hecht, 1976). Length-at-50%-maturity for both sexes was determined by two different techniques:

1. a visual estimate of the percentage maturity versus size class distribution to determine the smallest class in which 50% of the individuals were mature (Hecht, 1976) and
2. by fitting a logistic equation (Punt and Leslie, 1991; Butterworth *et*

al. 1989) of the form:

$$Y = \frac{1}{1+\exp(-(X_{mid}-X_{0.5})/\delta)} \qquad (1)$$

where Y is the proportion of mature fish in length class X, X_{mid} is the midpoint of the class interval X, $X_{0.5}$ is the length-at-50%-maturity and δ is a parameter that determines the width of the maturity ogive. The parameters $X_{0.5}$ and δ were estimated by a nonlinear least squares technique. Weighting factors used in the regression are N/Y(1-Y) where N is the number of observations in each size class X (Somerton, 1980) and Y is the proportion of mature fish. This assigns greater weight to those length classes in which more fish have been sampled. For those size classes that had proportions 0 or 1, the proportions were corrected by applying the formulae 0.25/N and (N-0.25)/N, respectively (Mikhayluk, 1985). This *ad hoc* transformation was performed in order that weighting factors could be calculated for these proportions. Tests were performed to determine how sensitive $X_{0.5}$ were to omissions of the 0 and 1 *ad hoc* transformed proportions. Standard errors estimated are asymptotic standard errors and are therefore approximate.

1.3 Results and discussion

The frequency of ripe running (stage 5) and spent plus resting (stages 7+8) female *S. commerson* is shown in Table I. Assuming that ripe running females are equally vulnerable to hook and line capture as compared to the other maturity stages, then the low frequency of ripe running females (stage 5) off Natal and Zululand (Table I) indicates that spawning does not occur in these regions but probably occurs off Mozambique - although the sample size from Mozambique is small, 17% of mature females were ripe running as compared to only 2% in Natal and Zululand, combined.

Further evidence that Natal and Zululand are not the principal spawning areas is shown by the high incidence of females (61%) in a post-spawning condition (stages 7 and 8) in these areas while in Mozambique only 28% of mature females were in a post-spawning state (Table I). It is, therefore, possible to postulate that the main spawning of *S. commerson* occurs off Mozambique, after which females then migrate south into the waters of Natal and Zululand. The latter is suggested by the high percentage of mature females in a post-spawning state as compared to a ripe running state in the latter regions (Table I). More intensive sampling or a tag and recapture study in Mozambique may confirm this. Similar observations to the above were also made for the species *Scomberomorus plurilinaetus* off the coasts of Natal and Zululand (van der Elst and Collette, 1984).

Table I Frequency of reproductive maturity stages in female *S. commerson* captured by hook and line in three adjoining regions along the South East coast of southern Africa.

REGION	MATURE ♀	STAGE 5	STAGE 7+8
	n	n(%)	n(%)
Mozambique	87	15(17)	24(28)
Zululand	356	3(0.8)	226(63)
Natal	230	7(3)	159(69)

The monthly percentage occurrence of each female gonad development stage of *S.*

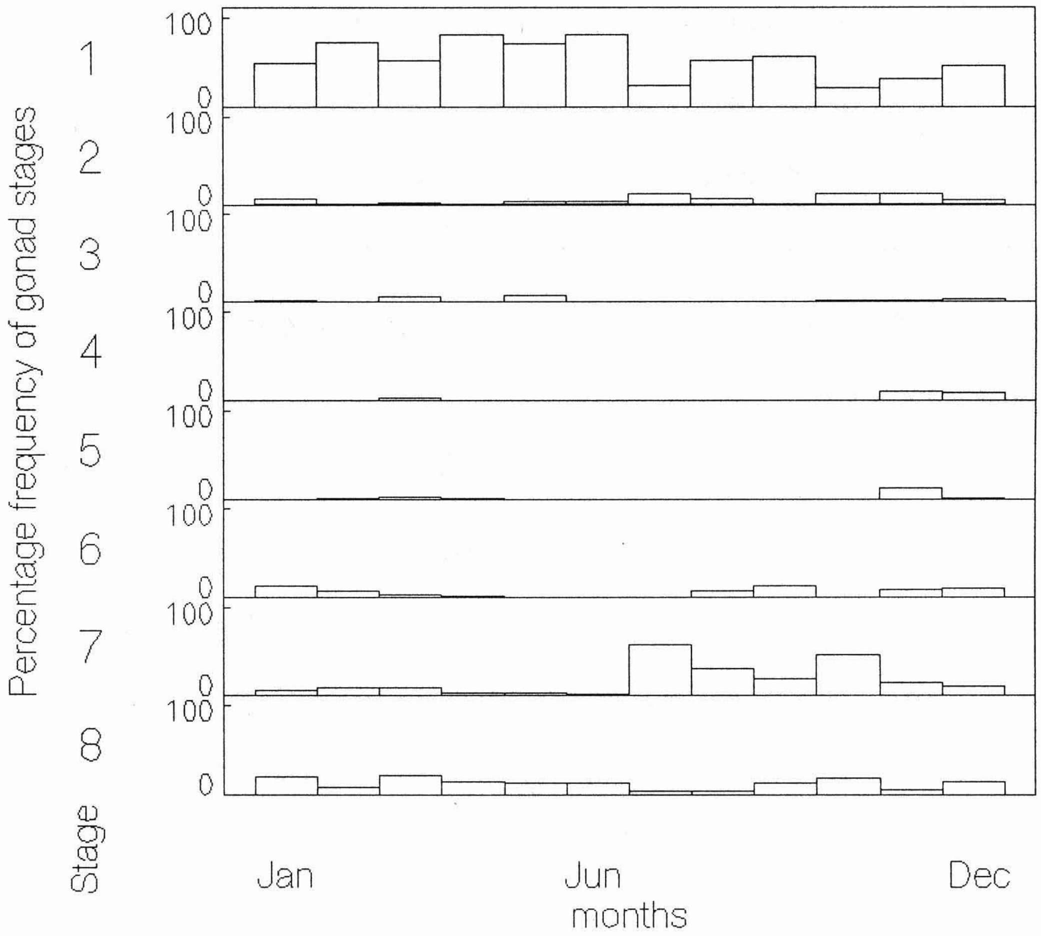

Figure 1 The occurrence of female gonad development stages in *S. commerson* from the S E coast of Africa expressed as a percentage of monthly samples (n = 1093).

commerson is shown in Figure 1. The occurrence of ripe running females (stage 5) over the summer season indicates that spawning occurs over a protracted time from November to March. In the waters off Zanzibar, *S. commerson* displays protracted spawning ranging from October to July (Williams, 1962). He further suggests that *S. commerson* can breed anytime of the year but with peaks at certain times of the year. Off Madagascar, *S. commerson* spawns from December to February (Collette and Nauen, 1983). Off the coast of India, Deveraj (1981) also found *S. commerson* to be a protracted spawner. The Florida king mackerel (*S. cavalla*) also displays protracted spawning of multiple frequency (Beaumarriage, 1973). It can, therefore, be concluded that king mackerel is a protracted spawner with spawning occuring over the spring-summer season.

A comparison of the regression slopes of ovary mass on somatic mass revealed that the slopes were significantly different ($F_{3,193}=172$ $p < 0.05$) for the various maturity stages (Figure 2). The log-log transformation of ovary mass versus fork length yielded slopes that were also significantly different ($F_{4,283}=122.5$ $p < 0.05$) for the various maturity stages (Figure 2).

The assumption that the linear relationship between ovary mass and body size is constant for different maturity stages in *S. commerson* is, therefore, violated and the GSI cannot be applied as a valid index of gonadal maturation in *S. commerson*. The breeding season as determined by macrostaging cannot be confirmed using the GSI.

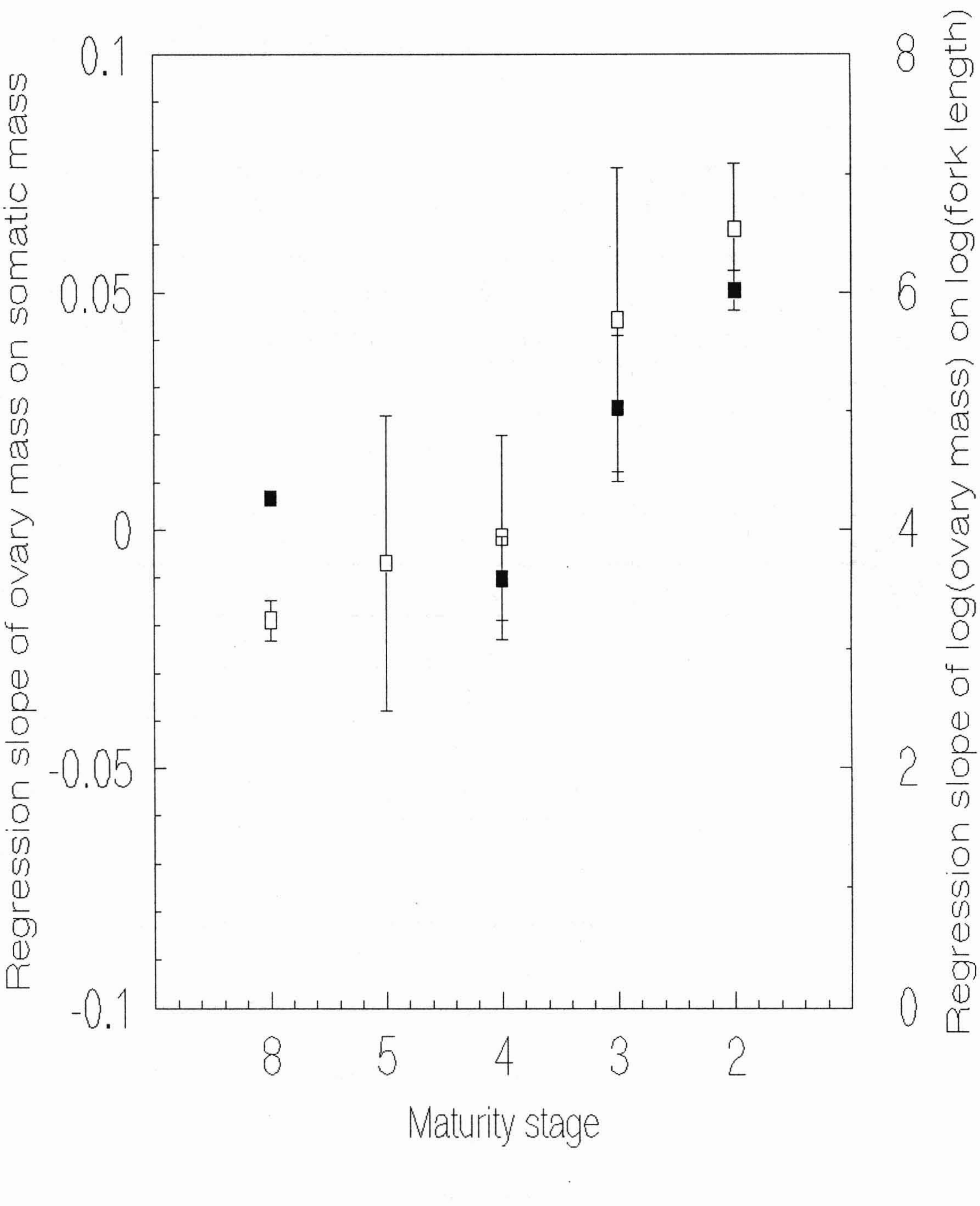

Figure 2 The test of regression parallelism for maturity stages 2 to 5 and 8 for female *S. commerson*. Empty and solid squares represent the ovary mass-fork length and ovary mass-somatic mass slopes respectively.

Examination of the maturity distribution for *S. commerson* (Table II) indicates that both sexes do not show a clear successive increase in the proportion of mature fish with increased length or that 100% maturity is attained.

Table II Percentage mature female and male *S. commerson* sampled along the south east coast of southern Africa from 1972 to 1991.

FORK LENGTH MIDPOINT(mm)	FEMALES		MALES	
	NUMBER	% MATURE	NUMBER	% MATURE
450	2	0	1	0
550	10	0	17	5.9
650	72	0	40	42.5
750	226	8.4	115	68.7
850	331	16.3	161	78.9
950	253	28.5	136	72.1
1050	137	51.1	70	78.6
1150	60	56.7	37	97.3
1250	37	59.5	17	82.4
1350	16	81.3	4	75
1450	5	40	1	100

Four possible factors could have contributed to the above distribution (Table II):

1. poor sampling of certain length classes,
2. certain individuals of some year classes mature earlier as opposed to late maturity in other year classes,
3. variable growth rates of individuals of different year classes resulted in variable maturity (Trippel and Harvey, 1991), or
4. there was some error in the assigning of gonad maturity stages eg.

mature stage 8 individuals could have been misclassified as immature stage 1 individuals or vice versa as it is often difficult to distinguish between these stages (Rudy van der Elst, Oceanographic Research Institute, pers. comm.).

The length-at-50%-maturity for female *S. commerson* based on a visual assessment of the maturity distribution ranges from 1000 to 1100mm (Table II) but it is possible that the length-at-50%-maturity may extend well above this class range. This is evident by the marginal increase in percentage maturity in the size classes 1150mm and 1250mm (Table II). The length-at-50%-maturity for male *S. commerson* determined by visual assessment of the maturity distribution ranges from 700 to 800mm. It is evident that males mature at a smaller size than female *S. commerson*. Length-at-50%-maturity for female and male *S. commerson* determined by the weighted logistic regression (equation 1) are shown in Table III.

Table III. Estimates of the parameters and their standard errors fitted to equation 1 for maturity data of both sexes of *S. commerson*. Values in bold are estimates when maturity proportions 0 and 1 were omitted from the regression. * - parameter values that best describe the maturity data.

PARAMETER	MALES			FEMALES		
	VALUE	s.e.	r^2	VALUE	s.e	r^2
δ	145* **144**	34.2 **40.9**	0.798 **0.794**	164.8 **155***	28.3 **19.7**	0.846 **0.926**
$X_{0.5}$	705* **706**	37.3 **44.7**		1102 **1096***	36.4 **25.5**	

The logistic equation (1) provides a curve that reasonably fits the maturity data for female *S. commerson* (Figure 3a). Removal of the *ad hoc* corrected zero and one proporptions for the maturity data of female *S. commerson* resulted in a superior fit (Table III, Figure 3a). This is indicated by the lower standard errors of the estimated parameters and by the higher coefficient of determination (r^2) value (Table III). The maturity data of male *S. commerson* is poorly represented by the logistic curve since only a few of the weighted points (especially those at the upper extremity of the curve) lie near the fitted curve (Figure 3b). This is a result of the low samples of males in the larger length classes. The parameter estimates of equation (1) for males were insensitive to omission of the weighted zero and one *ad hoc* transformed proportions (Table III). Imposing a minimum size limit to protect the spawning stock based solely on the length-at-50%-maturity may not sufficiently protect the spawning stock because the maturity of both sexes is variable over a range of lengths. Further, a minimum size set above the length-at-50%-maturity for females will substantially reduces catches in Natal since the peak modal class (900 to 1000mm, both sexes) of the exploited distribution falls below the length-at-50% maturity (Table III)(this aspect is discussed further under the yield-per-recruit section).

The above biological parameters will be used in the following sections (yield-per-recruit and growth analysis) as input parameters from which management options for the stock will be developed.

1.4 SUMMARY AND CONCLUSIONS

The principal spawning area for *S. commerson* is likely to be to the north of Natal, probably Mozambique, with spawning occurring over a protracted time over the spring-summer season (November to March). Off Natal and Zululand, 61% of mature females captured are in a post-spawning condition, which probably indicates that the migration into these waters from Mozambique is a post-spawning, feeding migration. Male king mackerel mature at a smaller size (706mm) as compared to females (1096mm). Both sexes show only marginal increases in percentage maturity with an increase in size class and 100% maturity is not attained. This is probably a result of a combination of factors, such as, difficulty in classification of immature and resting gonad stages and variable maturity dates as a result of differential growth rates.

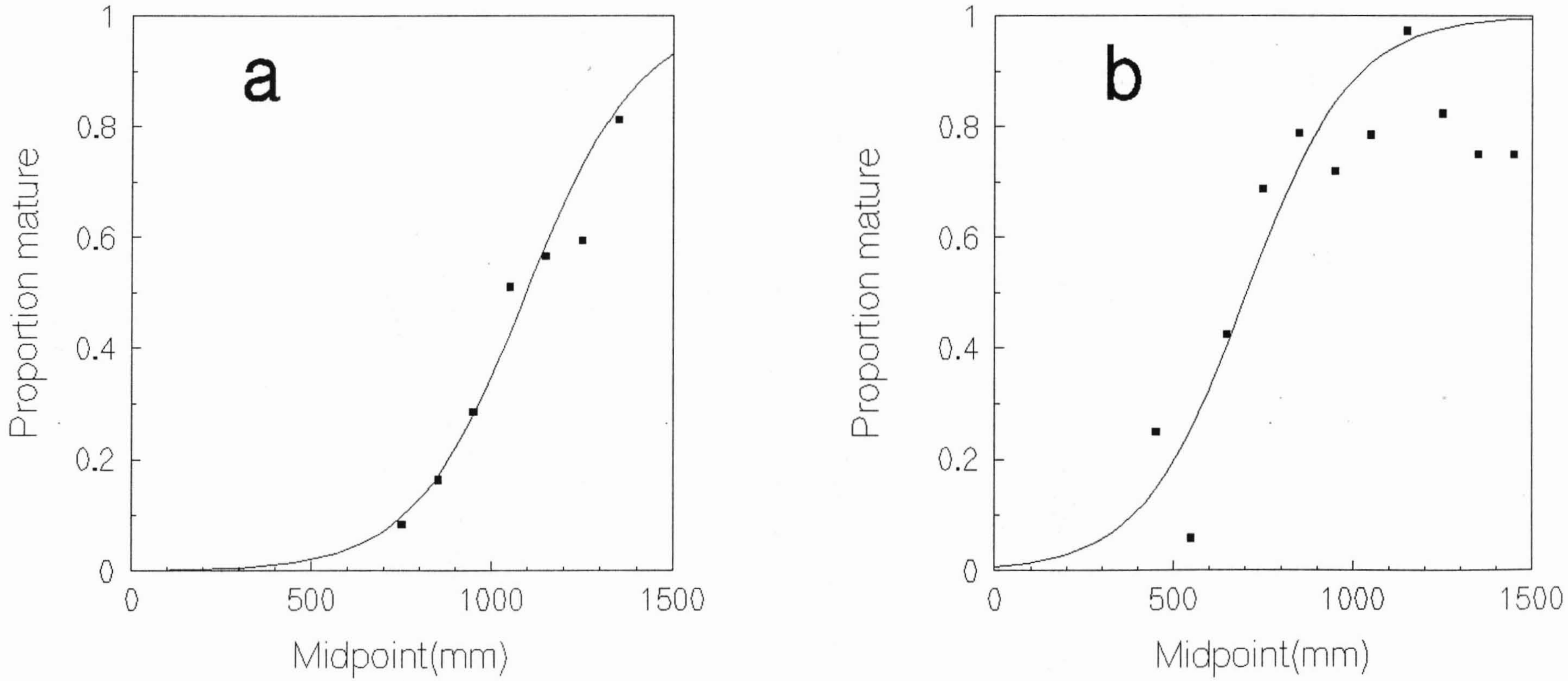

Figure 3 Fit of the logistic equation (1) to maturity data of female (a) and male (b) *S. commerson*. The parameter estimates of equation (1) are shown in Table III.

CHAPTER TWO

2. SOMATIC RELATIONSHIPS

2.1 Introduction

The relationship between mass(W) and length(L) in fishes can generally be expressed by the power relationship (Weatherley, 1972; Ricker, 1975):

$$W_i = aL_i^b \qquad \textbf{(1)}$$

where the data is of the form $\{(L_i,W_i):i = 1,...,n\}$ and a, b are constants that are specific to each species. The exponent b ranges from 2.5 to 3.5 in fishes and when equal to three it indicates isometric growth (Pauly, 1984).

Equation 1 is usually computed so that a predicted mass can be estimated from an observed length (length is quicker and more precisely measured than mass (Anderson and Gutreuter, 1983)). The a and b parameters of equation 1 are also input parameters to the yield-per-recruit model (Butterworth *et al.* 1989).

The parameters a and b, traditionally, are estimated by transforming equation 1 into a linear regression by taking logarithms (to base 10) on both sides of the equation i.e.

$$\log W_i = b\log L_i + \log a \qquad \textbf{(2)}$$

where the parameters are defined as in equation 1. The constants a and b are then estimated from ordinary least-squares regression but the application of an ordinary least-squares regression only approximates the estimates of a and b and results in unreliable standard error estimates (Pauly, 1984). Pauly (1984) further advises that nonlinear techniques of estimating a and b should be considered.

Ricker (1973) has advocated that a geometric mean functional regression should be fitted to equation 2 rather than an arithmetic linear regression. This option was rejected in this study for the following reasons: the geometric mean functional regression is used to determine the "central" relationship between variables that have been subjected to independent measurement errors (Ricker, 1973; Butterworth *et al.* 1989). To fit a data set to a functional regression requires some knowledge of the ratio of the error variances of the variables (Pope and Shanks, 1982; ICES, 1985) which can lie anywhere between zero and infinity and since this ratio cannot be determined from the data (ICES, 1985), this option was rejected. In fact, Pope and Shanks (1982) do not recommend the use of the geometric mean functional regression at all.

This study, therefore, investigates the above by evaluating the various regression techniques, fitted to data of *S. commerson*. The total length-fork length relationship is computed to facilitate the conversion of different length measurements that are commonly recorded. For example, minimum size limits of currently managed species are based on total lengths, the Sedgwick's/ORI Tagging Programme uses fork lengths while research bodies eg. Oceanographic Research Institute record both fork and total lengths. In this study it was difficult to obtain whole specimens of *S. commerson* from commercial fishermen because of its high market value or from recreational fishermen because it is a highly prized table fish. However, most were willing to part with the head region of their catch. This allowed the easy removal of the sagittal otoliths for age determination and a recording of the maxillary length was taken as an estimate of the size of the fish. The fork length-maxillary length relationship was, therefore, computed to estimate fork lengths from the maxillary length recordings.

2.2 Materials and methods

Length and mass data (n=2048) for *S. commerson* were collected on an irregular basis from 1972 to 1991. Maxillary length (from the tip to the most posterior part of the upper jaw) was measured by vernier callipers to the nearest 0.01mm. Total and fork lengths were recorded to the nearest millimetre for small specimens while large specimens were recorded to the nearest 0.5 cm (converted to millimetres for the analysis). Mass was measured to the nearest 0.1g for very small specimens; intermediate sized specimens were measured to the nearest 1g while large specimens were measured to the nearest 0.1kg (this was later converted to grams). The total length-fork length relationship for *S. commerson* was described using ordinary least-squares regression.

The fork length-maxillary length relationship was fitted to both a linear regression and an exponential model of the type:

$$FL_i = A + B\left(R^{ML_i}\right) \tag{3}$$

where FL_i and ML_i are the fork length and maxillary length of the i'th fish, respectively and A,B, and R are constants. Equation 3 was chosen to describe the fork length-maxillary length relationship because a scatter plot (Figure 2) of the variables with maxillary length as the independent variable showed a curvilinear relationship similar to the Von Bertalanffy growth equation. In fact, equation 3 is actually a "reparameterisation" of the Von Bertalanffy growth equation because the parameters A,B and R may be expressed in terms of the Von Bertalanffy parameters (Ratkowsky, 1986). Estimates of the parameters of equation 3 were obtained using the statistical package GENSTAT which obtains parameter estimates using a modified Newton method (Genstat 5 committee, 1988). The independent variable, maxillary length was scaled in order to avoid problems of having too small or too large a range of values which would lead to difficulties of estimation near the boundary of the allowed range of R.

Estimates of the parameters of the mass-length relationship for *S. commerson* (equation 1) were determined by two different techniques: ordinary least-squares regression of the log-transformed equation 2 and a modified Gauss-Newton algorithm (a nonlinear estimation technique) was used to estimate the parameters of equation 1 (Genstat 5 committee, 1988). The standard errors computed in the nonlinear techniques are asymptotic standard errors and are only approximate. A log-likelihood ratio test (Draper and Smith, 1966) was used to evaluate whether a better fit to the mass-length relationship could be obtained with the sexes separate than with the combined sexes (the test was performed on the log-transformed mass-length relationship).

A plot of the residuals *versus* fitted values (for all regressions) was visually inspected to determine if the residuals were normally distributed and homoscedastic (Butterworth *et al.* 1989).

2.3 Results and discussion

The fork length-total length relationship (for the range 190 to 1462mm, FL) is described by the following equations:

$$TL_i\,(mm) = 1.09\,(FL_i\,(mm)) + 32.6 \qquad r^2=0.938 \quad (n=374) \qquad \mathbf{(4)}$$

where TL_i and FL_i are the total length and fork length of the i'th fish, respectively. The s.e. of the slope is 0.0145 and that of constant is 14.5, and

$$FL_i\,(mm) = 0.86\,(TL_i\,(mm)) + 32.8 \qquad r^2=0.938 \quad (n=374) \qquad \mathbf{(5)}$$

where the variables are defined as in equation 4 and the s.e.'s of the slope and constant are 0.0115 and 12.8 respectively. Equation 4 is used to convert fork length into total length estimates while equation 5 is used for the reverse. In predictive linear regressions only the dependent variable is assumed to be subject to error and since both total and fork lengths are subject to error, two equations for the total length-fork length relationship have been described as outlined by Pope and Shanks (1982).

Table I. Estimates of the parameters of equation 1 and 2 fitted to the mass-length data (n=2048) as well as parameter estimates of equation 3 fitted to the fork-length-maxillary length data set (n=319) for *S. commerson*.

EQUATION	r^2	PARAMETER	VALUE	STD ERROR
(1)	0.945	a	0.1353×10^{-5}	0.158×10^{-6}
		b	3.2515	0.0166
(2)	0.939	log(a)*	-5.4066	0.0515
		b	3.0947	0.0175
(3)	0.932	A	2114.3	96.6
		B	-2374.3	68.9
		R	0.992991	5.68×10^{-4}
* this corresponds to an "a" estimate of 0.39×10^{-5}				

When a predictive linear regression was fitted to the fork length-maxillary length data set, examination of the residual plot revealed a convex shaped curve signifying that the residuals were not distributed normally (Figure 1). No presence of a systematic trend was evident in the residual plot when the latter data were fitted to equation 3. This equation was, therefore, used to describe the fork length-maxillary length relationship. The estimates of the parameters of equation 3, fitted to the fork length-maxillary length relationship (Figure 2), are summarised in Table I. Note that R is close to one. The parameter R cannot be set to one as this would result in equation 3 being a linear regression. The parameter R was actually restricted to the range $0<R<1$ as this results in a curve corresponding to the law of diminishing returns (Genstat 5 committee, 1988).

Mass-length data of the separate sexes, fitted to equation 2, were not statistically superior ($F_{2,1925} = 2.16$; $p < 0.05$) to that of the combined set. Williams (1962) also

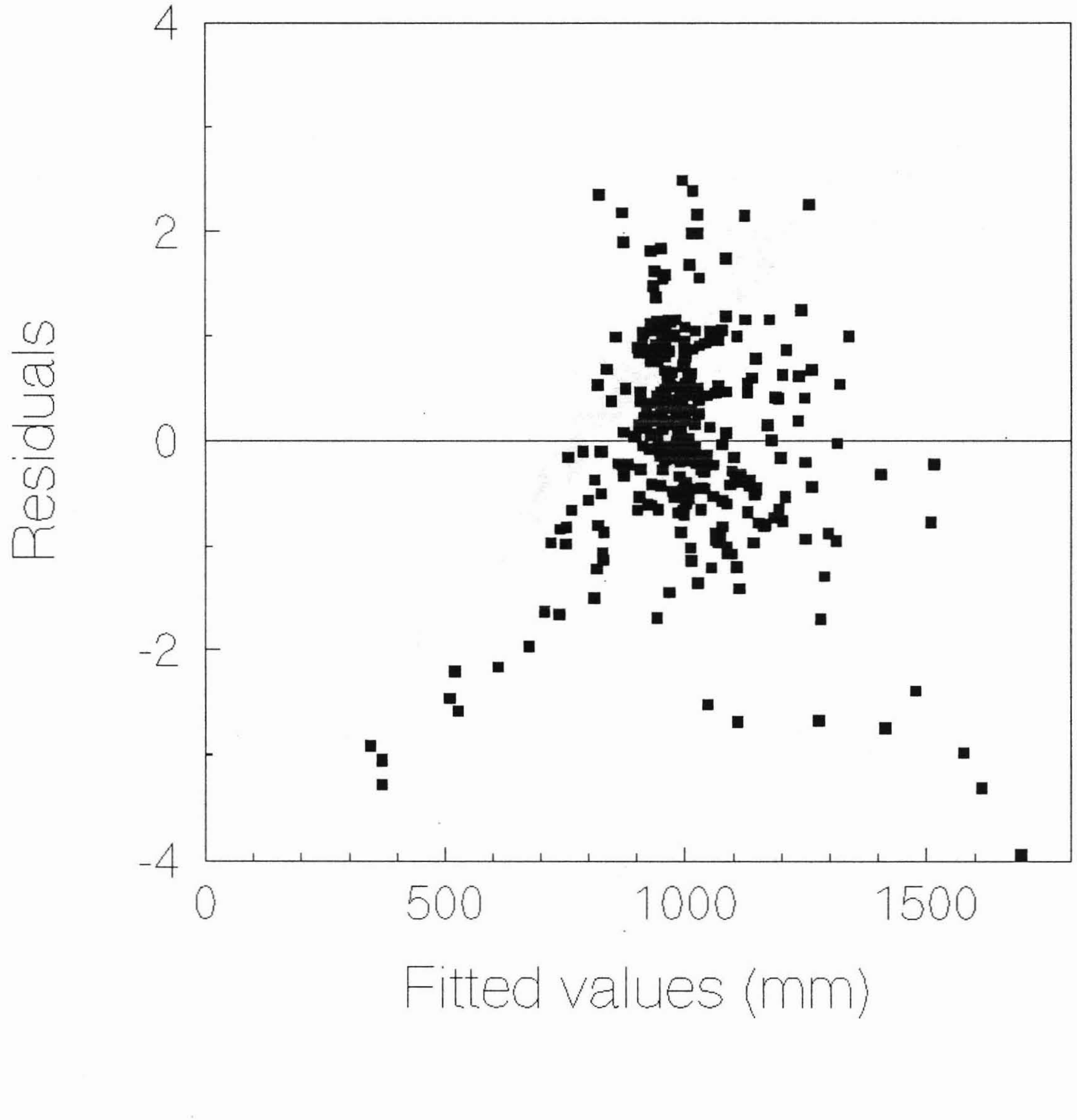

Figure 1 Residual plot when a linear model was fitted to the *S. commerson* fork length-maxillary length data set.

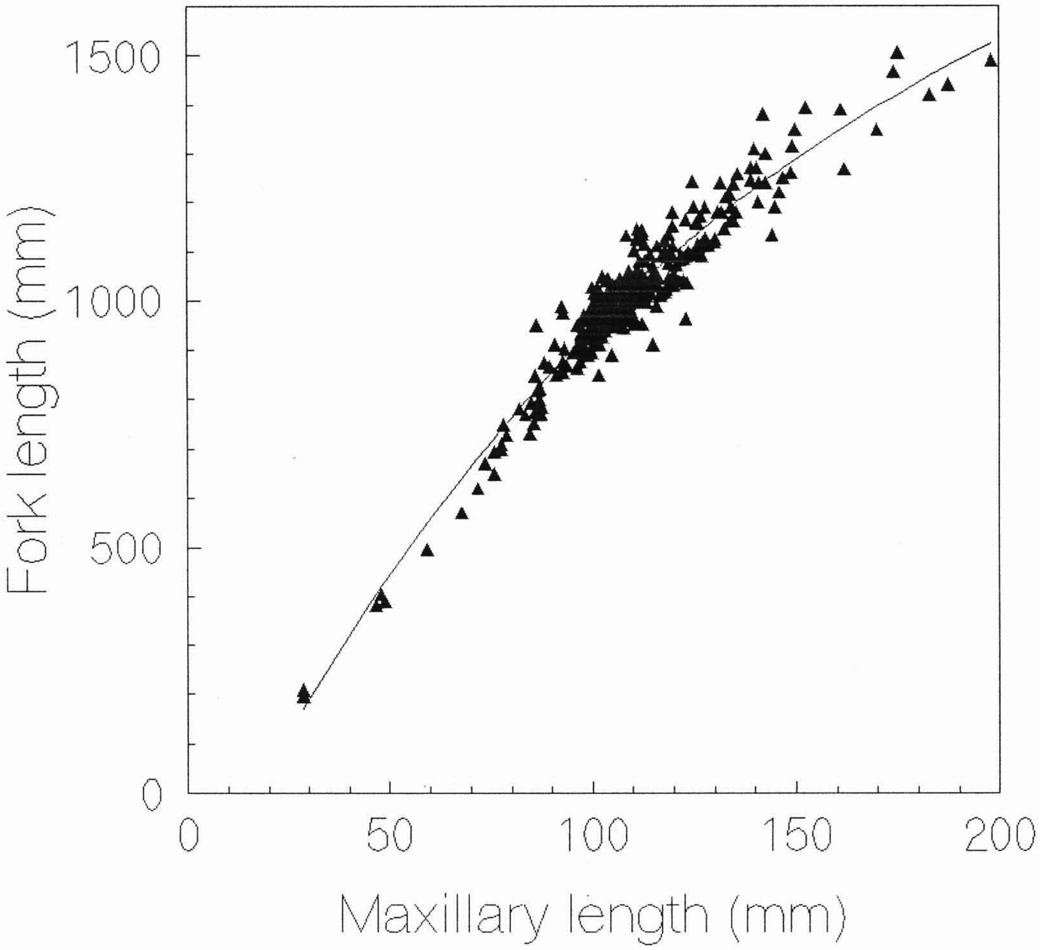

Figure 2 Fork length *versus* maxillary length relationship for *S. commerson* (both sexes combined n=319).

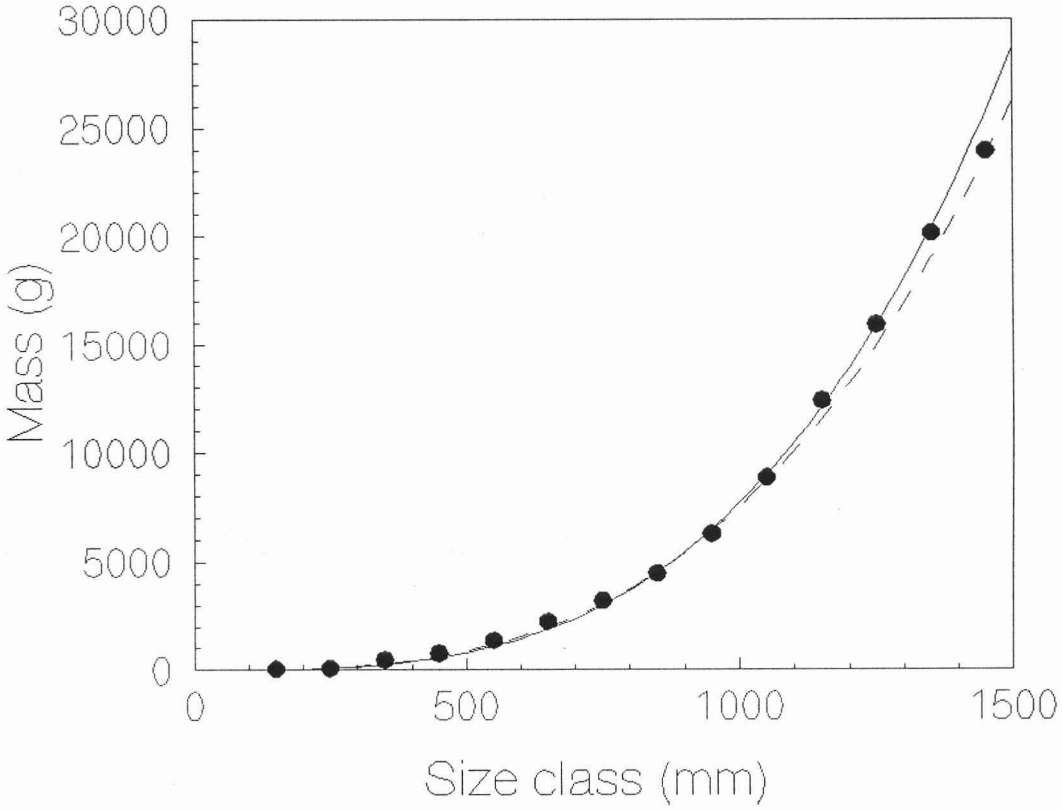

Figure 3 Mass *versus* length relationship of *S. commerson*. The solid and dashed lines represent the nonlinear and log-transformed fits to equation (1), respectively. Closed circles are the observed mean masses.

found that there was no significant difference in the mass of the two sexes at any given length. The mass-length data were, therefore, pooled for all subsequent analyses. The estimates of the parameters of the mass-length relationship (Figure 3) for both sexes of *S. commerson* are summarised in Table I. The nonlinear technique provided parameters that fit the data better than the log-transformed parameters. This is indicated by the higher r^2 value (Table I). Note also that the nonlinear curve (Figure 3) closely approximates the observed mean masses, especially in the exploited range of 1000+ to 1500mm, while the log-transformed curve generally underestimates the masses within this range. The nonlinear parameter estimates have, therefore, been applied to all subsequent analyses.

2.4 SUMMARY AND CONCLUSIONS

Two linear equations were fitted to the observed length data. These are used for the conversion of total length to fork length and for the reverse conversion. A curvilinear relationship best described the fork length-maxillary length relationship. This relationship will be utilised to convert maxillary lengths into fork lengths which are required in the age and growth study. Estimates of the a and b parameters of the mass-length relationship (equation 1) were obtained by a non-linear method and from the log-transformed version (equation 2). The former method provided parameter estimates that better describe the observed mass-length data.

CHAPTER THREE

3. THE LENGTH COMPOSITION OF THE CATCH

3.1 Introduction

Effective management of recreational and commercial fisheries is dependent on the collection and summarization of basic harvest data such as catch, effort, length distributions and biological characteristics of the exploited stocks. These data can be used to make a preliminary assessment of the stock status and its productivity or to evaluate impacts of regulatory measures on the resource. The most elementary data collected for the analysis of a fishery resource are length distributions and this chapter summarises the length statistics for *S. commerson*.

3.2 Materials and Methods

Length frequency data for *S. commerson* were sampled from 1972 to 1991 from commercial and sport catches off the coasts of Natal, Zululand and Mozambique. Samples of fish less than 400mm were obtained by research sampling during the same period - two juvenile specimens, which occurred in the bycatch of the prawn trawl fishery, off Mozambique, were provided by Dr Rui de Paula e Silva, Instituo de Investigacao Pesqueira, Maputo. Fork length was measured linearly from the tip of the snout to the fork of the tail and the sex was determined whenever possible. The Kolmogorov-Smirnov two-sample test (DeAlteris and Castro, 1991) was used to determine if there was any significant difference between the overall male and female length frequency distributions. The Student's t-test was used to determine if there was any difference between the mean size by sex (Zar, 1974). The overall sex ratio and sex ratio per length class were calculated and the chi-square test was used to determine if these ratios differed significantly from a 1:1 (male:female) ratio (Zar, 1974).

3.3 Results and discussion

3.3.1 Length distributions

Table I and Figure 1 summarise the overall length frequency distributions of *S. commerson* while Figure 2 summaries the monthly percentage distributions.

Females dominate the catch numbers per size class (Table I). However, the catch percentage per size class for each sex is the same (Table I). The Kolmogorov-Smirnov test statistic, therefore, indicated that there was no significant difference between the overall length frequency distributions of male and female king mackerel (95% confidence)(Figure 1).

The shape of a length frequency distribution is governed by recruitment, growth, mortality and sampling bias. In *S. commerson* it would be expected that the length frequency distribution would display multiple mode peaks since *S. commerson* displays rapid growth rates (Dudley *et al.*, 1992; McPherson, 1992; Bouhlel, 1986; Ingles and Pauly, 1984; Devaraj, 1981). Monthly length frequency samples of king mackerel, taken by gill nets, off Oman show at least three distinct cohorts (Dudley *et al.*,1992).

Table I. Length frequency distributions of *S. commerson* sampled off Natal, Zululand and Mozambique from 1972 to 1991. Samples less than 400mm were obtained from research sampling while the rest were obtained from commercial and sport catches.

size class (upper limit) (mm)	Females		Males		Both sexes	
	Number	Percent	Number	Percent	Number	Percent
0	0	0	0	0	0	0
100	0	0	0	0	5	0
200	1	0	0	0	5	0
300	0	0	0	0	1	0
400	0	0	0	0	1	0
500	2	0	2	0	11	1
600	12	1	20	2	41	3
700	84	5	53	5	166	13
800	281	16	178	18	677	24
900	509	29	269	28	1192	28
1000	386	22	226	23	1398	19
1100	217	12	132	14	940	6
1200	125	7	56	6	319	3
1300	77	4	25	3	160	1
1400	44	3	7	1	75	0
1500	13	1	1	0	23	0
1600	0	0	0	0	0	0
1700	1	0	0	0	3	0
1800	1	0	0	0	1	0
1900	0	0	0	0	0	0
2000	0	0	1	0	1	0

size class (upper limit) (mm)	Females		Males		Both sexes	
	Number	Percent	Number	Percent	Number	Percent
TOTAL	1753		970		5019	

However, in this study, the length frequency distributions are unimodal (Table I, Figures 1 and 2), indicating that there are potential sources of variation that result in the overlap between the sizes of individuals in successive age groups. There are two potential sources of variation in *S. commerson*. Variation in recruitment as a result of the protracted spawning displayed by *S. commerson* and variation in individual growth rates (see age and growth section).

The peak mode in the overall length distributions occurs at 900mm (male, female and sexes combined) (Table I, Figure 1). This same class peak is observed in the length frequency distributions for the months of June to November and April (Figure 2) while there is a shift to the 1000mm class interval during the rest of the months, except during December where the peak class is 800mm (Figure 2). It is clear that larger *S. commerson* are captured during the summer months, excluding December when relatively smaller fish are captured. The sharp decline in the descending limb of the length frequency distributions is probably due to the combined effects of emigration, a high mortality rate, gear selectivity and the fact that large king mackerel may be more difficult for anglers to land (Figures 1 and 2). The low samples in the months of June to October could possibly indicate that *S. commerson* is not abundant during these months. However, this is not clear, since poor weather conditions during these months, prevent the launching of boats and would therefore have resulted in low samples. This could not, however, be verified using CPUE data because effort in Natal's linefishery is directed not only to king mackerel but to many different species.

The exploited size range of *S. commerson* ranges from 402 to 1902mm and the mean

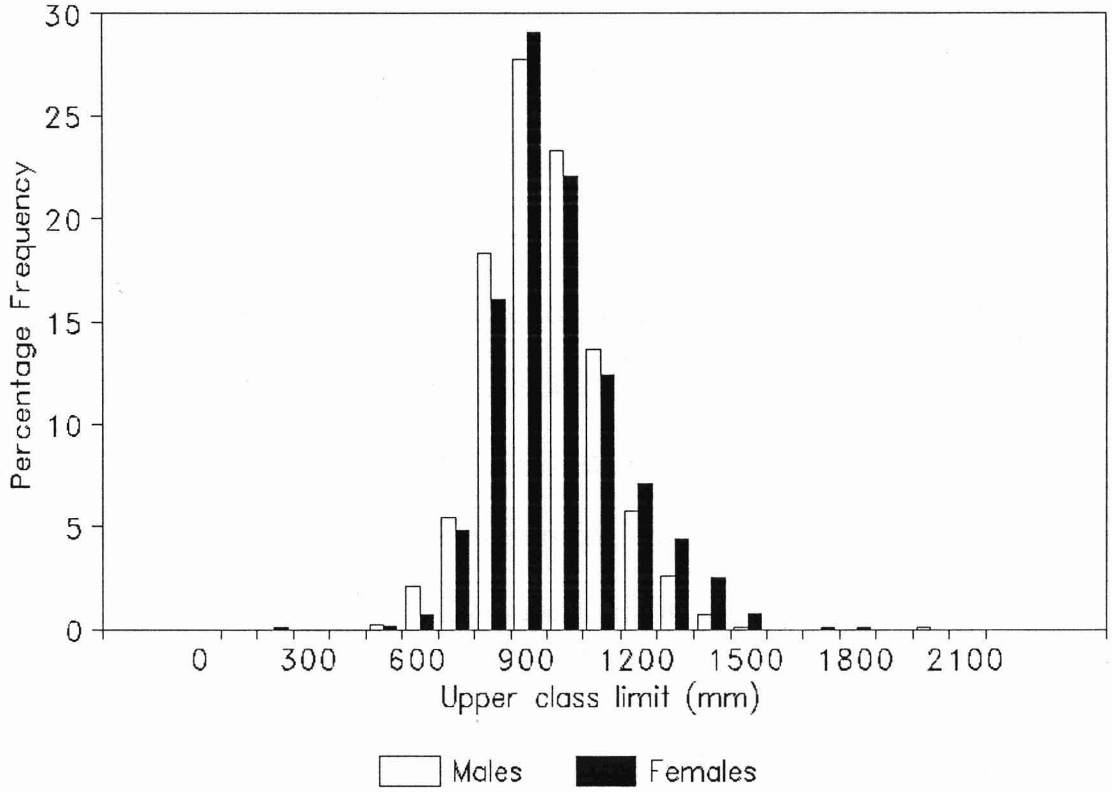

Figure 1 Percentage length frequency by sex of *S. commerson* sampled as indicated in Table I.

fork lengths and their 95% confidence intervals (in parenthesis) are: male 898mm(±9.7, n=970), female 926mm(±7.9, n=1753) and both sexes combined 934mm(±4.3, n=5019). There is, statistically, a significant difference between the mean fork lengths of males and females with the latter attaining a larger mean size ($P(|t| = 4.39) < 0.05$).

3.3.2 Sex ratio

Table II indicates the sex ratios (male:female) of *S. commerson* sampled. In the size class ranges of 700 to 1300mm, approximately twice as many females than males are being caught (Table II). Sex ratio increases with fish length (Table II). This indicates that large females are more vulnerable to capture than large males or that males do not attain large lengths. A possible reason for the latter is that if males exhibit a faster growth rate than females, the former will attain smaller mean asymptotic sizes than females (the strong correlation between the Von Bertalanffy K and L_∞ parameters account for this). McPherson (1992) found that male *S. commerson* had a larger K and smaller L_∞ parameter values when compared to females. The overall sex ratio of the catch is 1:1.81 (male:female) (Table II) and it differs significantly from a 1:1 ratio, assuming a random sampling of the population. In his study of king mackerel, Williams (1962) recorded a male to female sex ratio of 1:1.91 which was also a significant departure from the expected 1:1 ratio. The large chi-square values indicate that the sex ratios per size class also differ significantly from a 1:1 ratio (Table II).

This summary of the basic length composition of the catch will be utilised in the extraction of growth parameter estimates, mortality rate estimates and in the drawing up of a management plan for *S. commerson*.

3.4 SUMMARY AND CONCLUSIONS

The monthly and overall length frequency distributions of king mackerel are mainly unimodal in nature suggesting that king mackerel probably has variable recruitment as a result of its protracted spawning period or that there is large variation in individual growth rates or a combination of both. The peak mode in the overall length distribution occurs at 900mm. There is a significant difference between the mean sizes of the sexes with males attaining a smaller mean size than females; 898 and 926mm, respectively. The overall sex ratio is 1:1.81 (male to female) which indicates that approximately twice as many females than males occur in the catches.

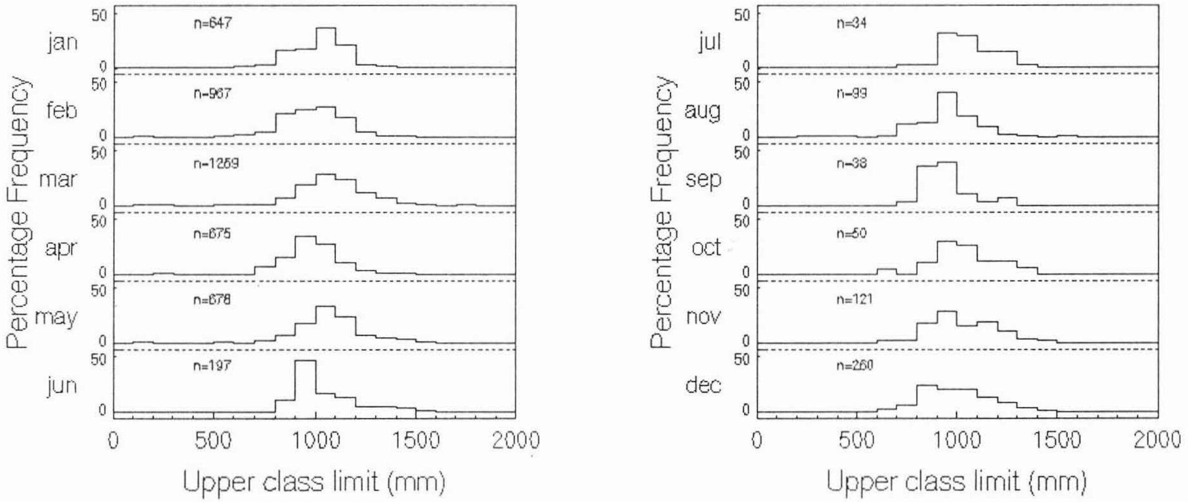

Figure 2 The monthly percentage length frequency distribution of *S. commerson* sampled from 1972 to 1991 off the south east coast of southern Africa.

Table II. The overall sex ratio (male:female) and sex ratio per length class of *S. commerson* sampled. Frequency data on which the chi-square statistic is calculated is shown in Table I.

size class (upper limit) (mm)	Sex Ratio	χ^2
0	-	-
100	-	-
200	-	-
300	-	-
400	-	-
500	1:1	0
600	1:0.6	2
700	1:1.59	7.01
800	1:1.59	23.11
900	1:1.89	74.04
1000	1:1.71	41.83
1100	1:1.64	20.70
1200	1:2.23	26.30
1300	1:3.08	26.51
1400	1:6.29	26.84
1500	1:13	10.29
1600	-	-
1700	-	-
1800	-	-
1900	-	-
2000	-	-
OVERALL	1:1.81	262.64

CHAPTER FOUR

4. AGE AND GROWTH

4.1 Introduction

The growth rate of an exploited species, is one of many input parameters to dynamic pool models such as the Beverton and Holt yield-per-recruit model (Beverton and Holt, 1957). To obtain an estimate of the growth rate requires some measure of biological time. Traditionally, this has been age which is obtained by counting seasonal bands or rings that are laid down in hard tissue such as scales or otoliths (Ricker, 1975). Another measure of biological time is size (Rosenberg and Beddington, 1988) with length being the simplest and most accurate to measure. Since age is a linear measure of time, age-structured assessment models have been preferred over the length-based models because length is a nonlinear measure of time and the conversion to a linear time-scale is not straight-forward (Rosenberg and Beddington, 1988).

Recently, however, there has been an upsurge in the application of length-based methods especially in the estimation of growth parameter estimates (Morgan and Pauly, 1987; Pauly, 1987; Shepherd, 1987; Basson *et al.*1988; Rosenberg and Beddington, 1988). The reason being, that unlike age data, large samples of length data can be obtained relatively simply and cheaply. Besides growth parameter estimates, length data can also be used to obtain mortality rate and gear selectivity estimates, for virtual population and yield-per-recruit analysis (Morgan and Pauly, 1987; Pauly, 1987). One of the most popular computer programs for obtaining Von Bertalanffy growth parameter estimates from length-frequency data is ELEFAN I (Pauly, 1987), but recently two new methods have been developed: Shepherd's Length Composition Analysis (SLCA) (Shepherd, 1987) and the Projection Matrix Approach (ProjMat) (Basson *et al.* 1988).

Growth parameter estimates for *S. commerson* in this study were obtained by two different methods: by fitting the Schnute growth curve (Schnute, 1981) to the age-length data to determine which submodel with a minimum of parameters adequately describes the data and from length-frequency data using SLCA. Both methods are described below.

4.1.1 SHEPHERD'S LENGTH COMPOSITION ANALYSIS

Shepherd's (1987) method uses length-frequency data to estimate the parameters of a Von Bertalanffy growth equation:

$$L_t = L_\infty(1-e^{-K(t-t_0)}) \tag{1}$$

where

L_t = mean length at age t,

L_∞ = mean asymptotic length,

K = rate at which L_t approaches the asymptote, and

t_0 = age at "zero" length.

The method requires as one of the inputs a range of the growth parameters (L_∞, K) which is chosen by the investigator *a priori*. A test function drawn from the given growth parameters then predicts the position of the modes and troughs on the length axis. This test function (T) is expressed as

$$T_L = \frac{\sin(\pi Q)}{\pi Q} \cos 2\pi (t_a - t_s) \qquad \textbf{(2)}$$

where $Q = (t_{max} - t_{min})$, t_{max} and t_{min} are the Von Bertalanffy ages that correspond to the upper and lower bounds of length interval L, respectively and $t_a = (t_{max} + t_{min})/2$. The season in which the sample is taken is represented by the parameter t_s and is expressed as a fraction of the annual cycle. The test function after a variance-stablizing square root transformation is then compared to the observed data, to score the possible combinations of L_∞ and K values. The score function (S) is calculated as

$$S = \sum_L T_L \sqrt{N_L} \qquad \textbf{(3)}$$

by summing over all length classes in the sample, where N_L is the observed number in each length class L. If there are more than one length-frequency sample then S values are summed over all the samples. A value of the goodness-of-fit score function that is large and positive for a given combination of growth parameters, indicates that these parameters fit the observed data well. Once the global maximum score function is determined, the precise identification of the values of the parameters L_∞ and K that correspond to local maxima of the score is achieved through the use of a function maximisation procedure based on the simplex method (Holden and Bravington, 1992). Shepherd (1987) showed that S is a periodic function (with the period equal to unity) of the Von Bertalanffy growth parameter t_0. He further showed that if S_0 is the value of S when $t_0 = 0$ and $S_{0.25}$ is the value of S when $t_0 = 0.25$, then the maximum of the score function is given by

$$S_{max} = \sqrt{(S_0^2 + S_{0.25}^2)} \tag{4}$$

and

$$t_0 = \frac{1}{2\pi}\arctan(\frac{S_{0.25}}{S_0}) \tag{5}$$

Once a given set of growth parameters has been chosen, the age composition of the length frequencies can be determined from the fitted growth curve (Holden and Bravington, 1992). This is achieved by using the growth curve to delineate the boundaries between the lengths at ages 0, 1, 2, etc., and the length frequencies at these boundaries are then "sliced" i.e. given estimates of L_∞ , K and t_0, and the time when the sample was collected t_s, for a length frequency distribution, then for each age i the lengths (L) corresponding to the midpoint between age i-1 and i and between ages i and $i+1$ are respectively

$$L_{i-0.5} = L_\infty(1-\exp(-K(i-0.5+t_s-t_0))) \tag{5}$$

and

$$L_{i+0.5} = L_\infty(1-\exp(-K(i+0.5+t_s-t_0))) \tag{6}$$

All lengths between $L_{i-0.5}$ and $L_{i+0.5}$ are then assigned age i. If $L_{i-0.5}$ and $L_{i+0.5}$ do not coincide with the length class boundaries then the number in a length class that is "sliced" by these cutoff lengths is apportioned to the lower and upper ages assuming a normal distribution of lengths in each length class.

4.1.2 SCHNUTE GROWTH MODEL

The fisheries biologist given a set of age-length data for a population usually faces two problems: which growth model to select and which method provides the most appropriate growth parameter estimates. There are several historical growth models that are commonly applied in fisheries science such as the Von Bertalanffy, Gompertz, Richards, logistic, exponential etc. models (Schnute, 1981). As there are many different growth models so there are also different methods employed to estimate the parameters eg. the Walford plot and various iterative procedures (Ricker, 1975). Usually the growth model and the parameter estimating procedure are selected subjectively by the biologist (Baker *et al.* 1991).

These problems were resolved by Schnute (1981) when he developed a generalised growth model that casts the above historical models and many others as submodels. This general growth model is derived from a concise biological principle that models growth acceleration as a linear function. The model allows for both accelerated and decelerated growth. The Schnute growth model is a four parameter model that describes fish size Y as a function of age t and the equation where the parameters a and b are not equal to zero is

$$Y_t = (y_1^b + (y_2^b - y_1^b)\frac{1 - \exp[-a(t-T_1)]}{1 - \exp[-a(T_2-T_1)]})^{1/b} \qquad \textbf{(7)}$$

Parameters y_1 and y_2 are the sizes corresponding to the two ages T_1 and T_2 (such as the youngest and oldest observed ages), respectively. The sizes y_1 and y_2 are chosen by the biologist and are usually mean sizes at age and estimates for these parameters are known fairly accurately by the investigator (most nonlinear parameter estimation procedures require good starting values that are sometimes unknown or difficult to obtain). Parameters *a* and *b* determine the shape of the growth curve. Parameter *b* controls the relative location of the inflection point of the curve along the size axis and given *b*, parameter *a* controls the relative location of the inflection point of the curve along the age axis. When $y_2 > y_1 > 0$ and $T_2 > T_1$ then equation 7 represents positive growth in size and not shrinkage. Based upon the values of the parameters *a* and *b*, the historical models are submodels of the Schnute growth curve eg. when $a > 0$ and $b = 1$ the special Von Bertalanffy growth submodel is defined.

4.2 Materials and Methods

Length frequency data and sagittal otoliths of *Scomberomorus commerson* were collected from commercial and recreational catches off Natal, Zululand and Mozambique on an irregular basis from 1972 to 1991. At times it was difficult to obtain whole specimens of king mackerel as it is a highly prized fish by both commercial and recreational fishermen, however most were willing to part with the head region of their catch. In these cases the maxillary length was taken as an estimate of the size of the fish. The maxillary lengths were later converted to fork lengths using the maxillary-fork length relationship (equation 3, Chapter 2).

Shepherd's (1987) Length Composition Analysis method was used to obtain estimates of the Von Bertalanffy parameters from the length frequency data. Monthly length frequency distributions for the various years were combined as this would reduce the effect of recruitment fluctuations during the sampling period (Holden and Bravington, 1992; Shepherd, 1987). Both SLCAI and SLCAII programs (Appendices A.1 and A.2 show the program listing, respectively) as well as the LFDA (Holden and Bravington, 1992) package were utilised in the analysis.

Age estimates were obtained from reading whole otoliths (n=637). Otoliths were immersed in ethanol and were read against a black background under a low power dissecting microscope using reflected light. The number of opaque bands was counted from the nucleus to the outer margin of the otolith. Each otolith was read twice by one reader with a minimum of one month between readings. If both readings of the same otolith coincided this was taken as the estimate. If the readings differed by one band then the average was taken as the estimate. If the readings differed by two or more bands the otolith readings were rejected.

Reproducibility of the age estimates was described by an index of average percent error (Beamish and Fournier, 1981) and the percent agreement technique (Kennedy, 1970). Although the latter is one of the commonest methods employed to compare the precision of a set of age determinations, Beamish and Fournier (1981) have critised this method on the grounds that it is independent of the number of age classes and hence cannot be used to evaluate the degree of precision equally for all species. They proposed, as an index, the average percent error (APE):

$$100[\frac{1}{N}\sum_{j=1}^{N}[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_{j}|}{X_{j}}]] \qquad \textbf{(9)}$$

where

N = number of fish aged,

R = number of times each fish is aged,

X_{ij} = *i*th age determination of the *j*th fish, and

X_j = the average age for the *j*th fish.

The APE is dependent on age and can be used to compare precision of different readers or different age sets as well as of different species (Beamish and Fournier, 1981). The percent agreement technique provides a measure of the actual agreement between age sets while APE measures the amount of variation between age sets. The lower the APE value the greater the precision. Appendix [A.3] includes a program listing in PASCAL which estimates the APE for different age sets.

Validation of the opaque band was achieved by visually examining the margin of monthly sampled otoliths (marginal increment analysis). It was then determined during which months (or season) that the opaque band was actively being laid down on the edge of the otolith (Hecht and Smale, 1986). This validation was further confirmed by using the growth equations derived from both the length- and age-based studies to predict the time-at-liberty of tagged recaptures. If the growth equations predict the time-at-liberty, then the assumption of the time period during which the opaque band is laid down is confirmed. The tag-recapture data were obtained from the Sedgwick's/ORI tagging programme and consisted of only two recaptures in which the length measurements could be verified.

The age-length data were fitted to the Schnute (1981) growth curve to determine if any submodels with fewer parameters could adequately describe the data (Butterworth *et al.* 1989). No attempt was made to fit growth curves to separate sexes as only few of the specimens from which otoliths were sampled were sexed. In order to determine which of the submodels of the Schnute curve is able to provide an adequate fit to the age-length data, a log-likelihood ratio test (Draper and Smith, 1966) was used to select between alternative fits. The error structure about the various growth curves was also modelled. It was assumed that the parameter constants of the various growth models describe the growth of the population, but allow for random variation or error. Two error structure situations were assumed: additive or multiplicative. In both cases, the error terms are assumed to be independent random variables following a normal distribution with mean O and constant variance σ^2. Parameter estimates were obtained by minimizing the residual sum of squares using the simplex method of function minimisation (Nelder and Mead, 1965). Estimates of the standard errors of the growth parameter estimates were obtained using the (conditioned) parametric bootstrap technique (Punt, 1989; Punt, 1988; Efron, 1981). 95% confidence intervals were obtained using the percentile method (Punt, 1992). The computer program PC-YIELD implements the above (Punt, 1992).

4.3 Results and discussion

4.3.1 LENGTH BASED METHOD

4.3.1.1 Shepherd's length composition analysis

L_∞ and K parameter ranges of 1200 - 1800mm and 0.1 - 0.5yr^{-1} were selected as initial input ranges, respectively. These ranges were based on Von Bertalanffy growth parameters derived from growth studies by other investigators (Table I). Examination of the length distributions in the sample (Table II) was also used to select the appropriate L_∞ range. These selected ranges were outside the Von Bertalanffy parameter estimates determined by Ingles and Pauly (1984) for king mackerel from the Philippines - their study was restricted to king mackerel $<$ 500mm which resulted in an underestimate of L_∞ and an overestimate of K.

Table III indicates the score function values using Shepherd's length composition analysis for a range of L_∞ and K parameter combinations for *S. commerson* sampled. From these ranges the highest score function was obtained for L_∞ = 1266.7mm and K = 0.46yr^{-1} but as indicated by the shaded areas of Table III a ridge of other possible L_∞ and K value combinations also show high values. Multiple maxima were observed in the response surface eg. at the parameter pairs (1333.3mm,0.41yr^{-1}) and (1533.3mm,0.23yr^{-1}) (Table III). These were considered as local maxima.

Table I. Von Bertalanffy parameter estimates for *S. commerson* derived by various investigators using different parameter estimation techniques. Lengths are fork lengths. * - total length to fork length conversions of Thiagarajan (1989)

L_∞(mm)	K(yr^{-1})	Method	Sex	Source
490	0.7	length-based	combined	(Ingles and Pauly, 1984)
1357*	0.2097	length-based	combined	(Bouhlel, 1986)
1871*	0.18317	age-based	combined	(Devaraj, 1981)
1100	0.1	length-based	combined	(Cheunpan, 1986)
1775	0.38	length-based	combined	(Thiagarajan, 1989)
1550	0.17	age-based	females	(McPherson, 1992)
1275	0.25	age-based	males	(McPherson, 1992)
2260	0.208	length-based	combined	(Dudley *et al.* 1992)
1936	0.292	length-based	combined	(Dudley *et al.* 1992)
1383	0.362	age-based	combined	(Dudley *et al.* 1992)
1312	0.614	length & age-based	combined	(Dudley *et al.* 1992)

This shaded ridge (Table III) may provide a rough approximation to the shape and size of the confidence region attached to the parameter estimates - the score function relative to the maximum is probably analogous to a variance ratio and the contour corresponding to half the maximum can be associated with a 95% confidence level (Shepherd, 1987). Table IV indicates the optimum t_0 values for each L_∞ and K pair.

Note that the value of t_0 is strongly dependent on the choice of L_∞ and K values. Based on the output of Table III the L_∞ and K ranges were then restricted to the ranges 1200 - 1300mm and 0.44 - 0.48yr^{-1}, respectively. Within these ranges the best L_∞ and K pair and t_0 was determined (using the simplex method) i.e. the growth parameter pair that produced the maximum score. The results were L_∞ = 1263.7mm, K = 0.4699yr^{-1} and t_0 = -0.877yrs (Score=24.07222). Note that in this analysis it was assumed that t=0 corresponds to January 1 and t_0 was restricted to -1 to zero. Therefore t_0 = -0.877yrs suggests that *S. commerson* would have zero length at the end of November, but the actual year cannot be estimated. It is for this reason that the Von Bertalanffy parameters estimated here, provide only relative and not absolute ages (Table V,VI).

The marginal increase in the cumulative scores indicates that the growth information is obtained from only a few length classes (700 and 900mm classes)(Table V); which suggests that the length frequency distributions for *S. commerson* are not suitable for the extraction of growth information. This is probably a result of the protracted spawning period displayed by *S. commerson* which obscures the modes in the distributions or it could be the result of poor sampling (the length classes from which the growth information are derived are also the best sampled - Table II,V).

Finally, the numbers at age corresponding to the same choice of growth parameters are given in Table VI. Experimentation with various good parameter choices (Table III,IV) shows that the numbers at age are strongly dependent on the choice of L_∞, K and t_0 values. Therefore, the utilisation of the age composition may not be suitable to estimate, for example, mortality rates or to forecast catches.

Despite these, Shepherd's length composition analysis provides reasonable K and L_∞ values which fall within the ranges of other length-based or age-based studies (Table I,III). However, it is not clear which single growth parameter pair best fits the data. The growth parameters chosen in this study (Table V,VI), were selected simply by the estimates that maximised the score. It is interesting to note that these two parameters, estimated from length-frequency data, fall well within the 95% confidence intervals for these parameters, that were estimated from age-length data (Table I,VII)(see sections below). From simulation studies, it has been shown that Shepherd's length composition analysis estimates the K value to at least 15% of its true value, given length data that displays some peaks and troughs. Further, the quality of the parameter estimates deteriorates as the variation in length-at-age increases (due to protracted spawning or different growth rates between individual animals) (Basson *et al.*1988). The length frequency data of *S. commerson*, although mostly unimodal in nature (Table II), display some variation in length-at-age because the peaks are not flat over a range of classes. Hence, reasonable parameter estimates were possible since the peak modes could reasonably be followed over time.

4.3.2 AGE BASED METHOD

4.3.2.1 Precision

Of the 637 otoliths read, 92 were rejected as unreadable. These otoliths were either broken, completely opaque or translucent. Of the remaining otoliths, readings were obtained for 73%. This percentage only includes those readings that coincided (37%) and those that differed by one band reading (36%). Those readings that differed by more than one band (27%) were excluded from the analysis. These latter readings comprised mostly of older fish were interpretation of the banding, especially on the margin, was difficult.

Table II Length-frequency data of S. commerson used in Shepherd's length composition analysis. The data have been combined for the years 1971 to 1991 to reduce recruitment variations. The length classes are lower limits.

Length Class (mm)	SEASON EXPRESSED AS FRACTIONS OF THE YEAR											
	0.08	0.17	0.25	0.33	0.42	0.50	0.60	0.67	0.75	0.80	0.90	1.00
0	1	1	2	0	3	0	0	0	0	0	0	0
100	0	0	2	2	0	0	0	1	0	0	0	0
200	0	0	0	0	0	0	0	1	0	0	0	0
300	0	0	0	0	0	0	0	1	0	0	0	0
400	3	1	2	0	4	0	0	0	0	0	0	1
500	8	14	4	1	2	0	0	1	0	2	2	6
600	23	42	14	46	12	0	1	11	1	0	2	14
700	105	195	89	105	50	21	1	12	10	5	23	63
800	107	240	232	234	119	91	11	40	11	15	37	54
900	232	257	353	181	225	33	10	19	3	13	20	53
1000	136	166	294	74	163	26	5	9	1	6	24	35
1100	20	40	138	19	46	9	5	2	2	6	13	20
1200	7	8	82	8	27	9	1	1	0	3	4	10
1300	4	3	32	5	19	6	0	0	0	0	3	3
1400	1	0	13	0	5	2	0	1	0	0	0	1
1500	0	0	0	0	0	0	0	0	0	0	0	0
1600	0	0	2	0	1	0	0	0	0	0	0	0
1700	0	0	0	0	1	0	0	0	0	0	0	0
1800	0		0	0	0	0	0	0	0	0	0	0
1900	0		0	0	1	0	0	0	0	0	0	0

Table III Matrix of normalised score values for a range of L_∞ and K values for *S. commerson* using Shepherd's length composition analysis. The elements were divided by the maximal score = 23.41855. The shaded cells indicate a ridge of high scores for possible L_∞ and K combinations.

	Value of K(yr^{-1})									
L_∞(mm)	0.10	0.14	0.19	0.23	0.28	0.32	0.37	0.41	0.46	0.50
1200.0	0.013	0.182	0.125	0.181	0.126	0.548	0.045	0.208	0.318	0.462
1266.7	0.110	0.189	0.244	0.143	0.429	0.391	0.215	0.317	1.000	0.737
1333.3	0.061	0.165	0.363	0.142	0.394	0.545	0.492	0.830	0.474	0.200
1400.0	0.130	0.133	0.214	0.341	0.628	0.439	0.767	0.276	0.336	0.250
1466.7	0.091	0.205	0.281	0.278	0.569	0.638	0.311	0.539	0.178	0.280
1533.3	0.404	0.290	0.141	0.831	0.466	0.325	0.553	0.213	0.194	0.437
1600.0	0.096	0.151	0.220	0.535	0.267	0.630	0.289	0.090	0.478	0.623
1666.7	0.158	0.359	0.715	0.167	0.472	0.467	0.233	0.426	0.441	0.502
1733.3	0.118	0.102	0.794	0.051	0.480	0.481	0.233	0.363	0.499	0.494
1800.0	0.196	0.339	0.369	0.321	0.682	0.094	0.263	0.446	0.428	0.550

Table IV Matrix of the Von Bertalanffy t_0 estimates for possible L_∞ and K parameter combinations for *S. commerson* using Shepherd's length composition analysis. The shaded cell indicates the t_0 value for L_∞ = 1266.7mm and K=0.46yr^{-1}.

	Value of K(yr^{-1})									
L_∞(mm)	0.10	0.14	0.19	0.23	0.28	0.32	0.37	0.41	0.46	0.50
1200.0	-0.649	-0.910	-0.764	-0.041	-0.252	-0.052	-0.748	-0.727	-0.061	-0.971
1266.7	-0.029	-0.622	-0.118	-0.172	-0.073	-0.863	-0.788	-0.223	-0.939	-0.708
1333.3	-0.890	-0.184	-0.897	-0.321	-0.925	-0.803	-0.211	-0.905	-0.677	-0.951
1400.0	-0.047	-0.068	-0.836	-0.091	-0.934	-0.363	-0.908	-0.820	-0.822	-0.658
1466.7	-0.403	-0.328	-0.757	-0.151	-0.618	-0.013	-0.895	-0.800	-0.477	-0.040
1533.3	-0.083	-0.170	-0.313	-0.956	-0.204	-0.983	-0.828	-0.592	-0.034	-0.007
1600.0	-0.970	-0.088	-0.518	-0.682	-0.011	-0.908	-0.731	-0.336	-0.021	-0.893
1666.7	-0.493	-0.976	-0.215	-0.296	-0.032	-0.817	-0.567	-0.041	-0.905	-0.906
1733.3	-0.239	-0.724	-0.983	-0.199	-0.936	-0.700	-0.093	-0.963	-0.909	-0.882
1800.0	-0.854	-0.956	-0.803	-0.109	-0.869	-0.521	-0.022	-0.926	-0.884	-0.929

Table V Relative age estimates obtained by "slicing" the length frequency data using the growth parameters L_∞ = 1263.7mm, K = 0.4699yr^{-1} and t_0 = -0.877yrs and truncating to conventional integer age groups relative to 1 January.

Length class(mm) (lower limit)	Age(yrs)	Cumulative Score
0	-0.88	3.29
100	-0.70	5.18
200	-0.51	6.01
300	-0.30	6.56
400	-0.07	9.00
500	0.19	9.75
600	0.49	-1.60
700	0.84	11.52
800	1.26	10.99
900	1.77	23.73
1000	2.46	23.80
1100	3.47	23.81
1200	5.48	-

Table VI Age composition of data in Table II, obtained through "slicing", using L_∞ = 1263.7mm, K = 0.4699yr^{-1} and t_0 = -0.877 yrs.

Age (yrs)	NUMBERS AT AGE PER SEASON											
	0.08	0.17	0.25	0.33	0.42	0.50	0.58	0.67	0.75	0.83	0.92	1.00
0	18	37	20	48	31	8	2	25	11	9	39	109
1	189	408	314	356	208	115	16	54	13	23	44	83
2	288	340	448	193	251	36	9	14	2	8	24	34
3	121	135	228	50	100	15	3	3	1	3	7	0
4	1	4	19	3	10	2	2	1	1	3	6	10
5	9	16	50	6	13	2	1	0	0	1	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0

The APE value calculated from the two set of age readings is 20.25%. McPherson

(1992) recorded an APE value of 0.9% for *S. commerson* in Queensland waters. It is clear that age determinations from the otoliths of *S. commerson,* in this study, are much less precise. Precision is used to describe the reproducibility of age estimates and does not imply that the estimates are accurate or inaccurate. Individual APE values which were high were obtained mostly from older fish where age readings differed by as much as 3 to 5 bands.

4.3.2.2 Validation

Validation of the opaque band in *S. commerson* by marginal analysis proved inconclusive - poor weather conditions prevent the launching of skiboats and resulted in the lack of adequate samples during August to October (Figure 1). Furthermore, in older fish it was often difficult to interpret the banding at the margin. It is possible that two opaque bands are laid down annually - a minor opaque band in May and a major one during the months of August to January (Figure 1). Devaraj (1981) in his study of *S. commerson* determined that the hyaline band was laid down four times a year (using marginal increment analysis) but in conjunction with modal (cohort) progression analysis of length frequency data he concluded that two hyaline bands were laid down per year. McPherson (1992) validated the opaque zone (the primary opaque zone as he terms it) as annual in one to three year old fish using marginal increment analysis but he also observed secondary opaque zones in conjunction with the primary opaque zone. He found that the secondary zones were more prevalent in mature females. In this study the available data indicated that the opaque band in *S. commerson* was laid down biannually and was confirmed using tagging data and the growth model. This

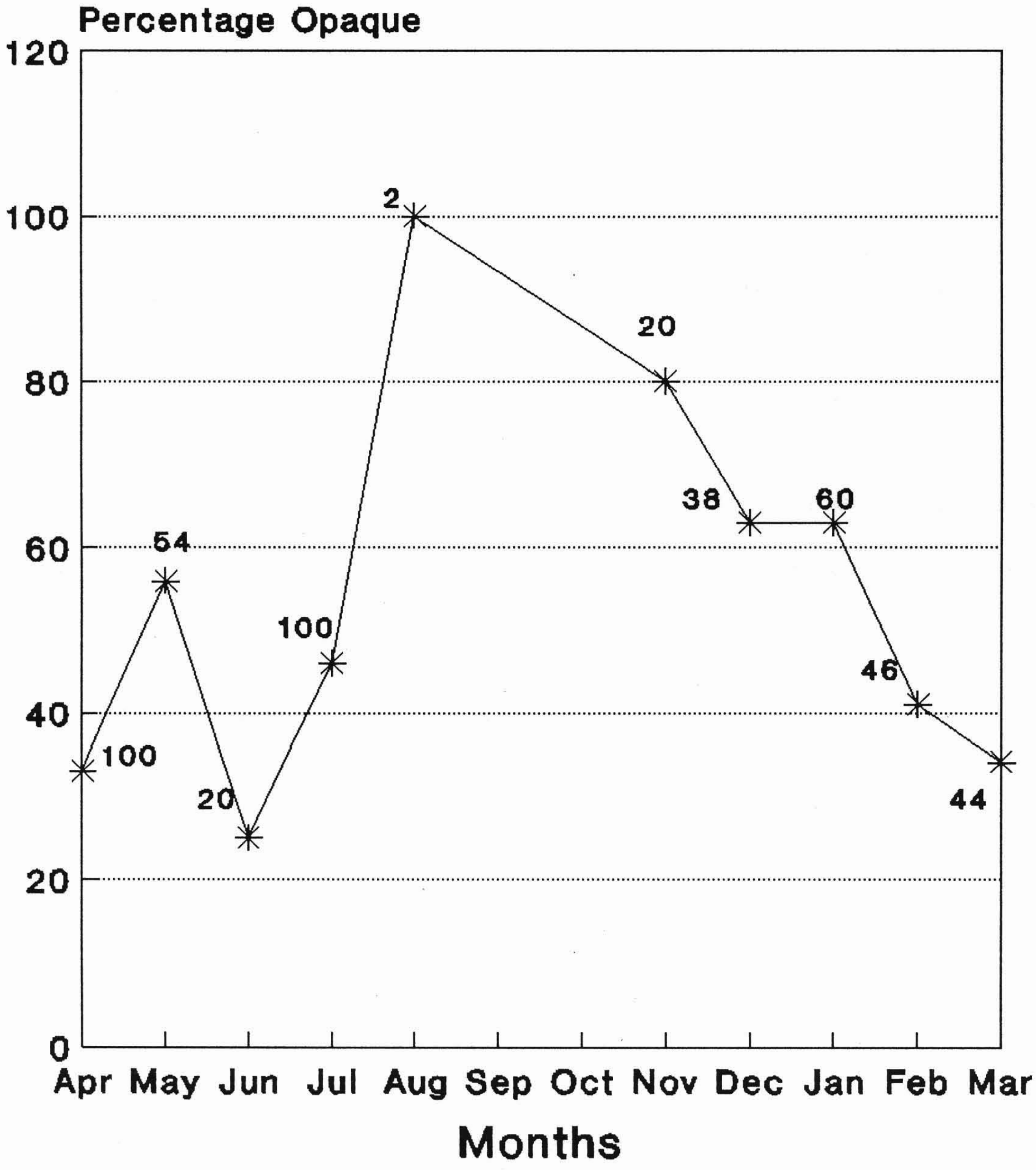

Figure 1 Percentage of *S. commerson* otoliths laying down an opaque band. Numbers are the monthly samples.

aspect is reported on in the following sections. Chemical marking of otoliths, for example, using the antibiotic tetracycline in a mark-recapture study will provide the most conclusive proof to this assumption but this is beyond the scope of this study.

4.3.2.3 Growth

The estimates of the parameters of the Schnute growth curve fit (equation 7) to the age-length data set (based on the assumption that the opaque band is laid annually or biannually), as well as their estimated standard errors (s.e.'s) and 95% confidence intervals, are given in Table VII. The parameter estimates, shown in Table VIIB, best describe the growth of *S. commerson*. These growth parameter estimates were chosen because they best predict the time-at-liberty of tagged individuals (see following section). All discussions and further analyses are, therefore, based on the parameter estimates given in Table VIIB unless stated otherwise.

Two submodels of the Schnute growth equation adequately model the growth of *S. commerson*: the generalised Von Bertalanffy as well as the special Von Bertalanffy (equation 1). Of these two fits the latter, was selected because it has fewer parameters and the fit of the generalised Von Bertalanffy equation was not statistically superior to that of the special Von Bertalanffy growth equation ($F_{1,388} = 0.996085$; $p < 0.05$).

Table VII Estimates of Schnute growth equation parameters, their s.e's and 95% confidence intervals. In the case of the special Von Bertalanffy fit no s.e. for b is reported since it is fixed. "A" reports the estimates assuming one opaque band is laid down annually while "B" reports estimates assuming that two opaque bands are laid down annually ($n=392$).

A

PARAMETER	VALUE	STANDARD ERROR	LEFT 95% C.I.	RIGHT 95% C.I.
Schnute Fit				
a	0.1237	0.0449	0.0313	0.2088
b	1.5087	0.2832	0.9304	2.2574
y_1 mm ($T_1=0$yrs)	781.56	12.31	754.24	807.60
y_2 mm ($T_2=10$yrs)	1213.40	28.73	1156.94	1265.90
Special Von Bertalanffy fit ($b=1$)				
a	0.1479	0.0400	0.0759	0.2321
y_1 mm ($T_1=0$yrs)	783.46	11.18	759.67	805.46
y_2 mm ($T_2=10$yrs)	1211.59	27.71	1161.60	1272.44
L_∞ (mm)	1338.00	119.30	1207.40	1692.10
K (yr^{-1})	0.1479	0.0400	0.0760	0.2321
t_0 (yrs)	-5.957	1.088	-8.612	-4.340

B

PARAMETER	VALUE	STANDARD ERROR	LEFT 95% C.I.	RIGHT 95% C.I.
Schnute Fit				
a	0.2230	0.0997	0.0616	0.4086
b	1.6244	0.4245	1.2356	2.1279
y_1 mm ($T_1=0$yrs)	782.65	12.15	756.64	807.35
y_2 mm ($T_2=5$yrs)	1218.34	30.67	1161.21	1283.42
Special Von Bertalanffy fit ($b=1$)				
a	0.2917	0.0825	0.1424	0.4593
y_1 mm ($T_1=0$yrs)	783.43	11.59	760.07	805.65
y_2 mm ($T_2=5$yrs)	1213.26	29.14	1160.07	1272.19
L_∞ (mm)	1343.50	131.30	1204.74	1716.21
K (yr^{-1})	0.2917	0.0825	0.1424	0.4592
t_0 (yrs)	-2.999	0.572	-4.475	-2.181

Estimates of the growth parameters, their s.e.'s and 95% confidence intervals of the special Von Bertalanffy model, are given in Table VII. Figure 2 shows the fit of the special Von Bertalanffy growth function to the age-length data of *S. commerson*, based on the estimates provided in Table VIIB. As the variance of length-at-age, for all the growth models fitted, increases with age, the relative error model (Punt, 1992) was selected when fitting the growth curves to the data in order that the residuals were homoscedastic.

The L_∞ parameters of the special Von Bertalanffy growth equation are imprecisely determined - note the large s.e. (Table VII). This is a result of a lack of data points in the older-larger classes. The very small t_0 values (Table VII) are a result of the protracted spawning of *S. commerson*, which results in a wide length range (600 to 900mm) of 0+ year old king mackerel (Figure 2). Zero to one year old fish are approximately half the maximum mean attainable size (L_∞)(Table VIIB,Figure 2). This indicates a very rapid growth rate during this stage. Rapid growth of young *S. commerson*, similar to this study, has been reported from Australia (McPherson 1992) and Oman (Dudley *et al.* 1992). The K parameter is reasonably well estimated as compared to the L_∞ and t_0 parameters (Table VII). This is understandable since the latter two are actually extrapolations of the data.

4.3.3 SELECTION OF THE BEST GROWTH PARAMETERS

To select the growth parameters (derived from the length- and aged-based growth study) that best describe the growth of *S. commerson*, the observed time-at-liberty for

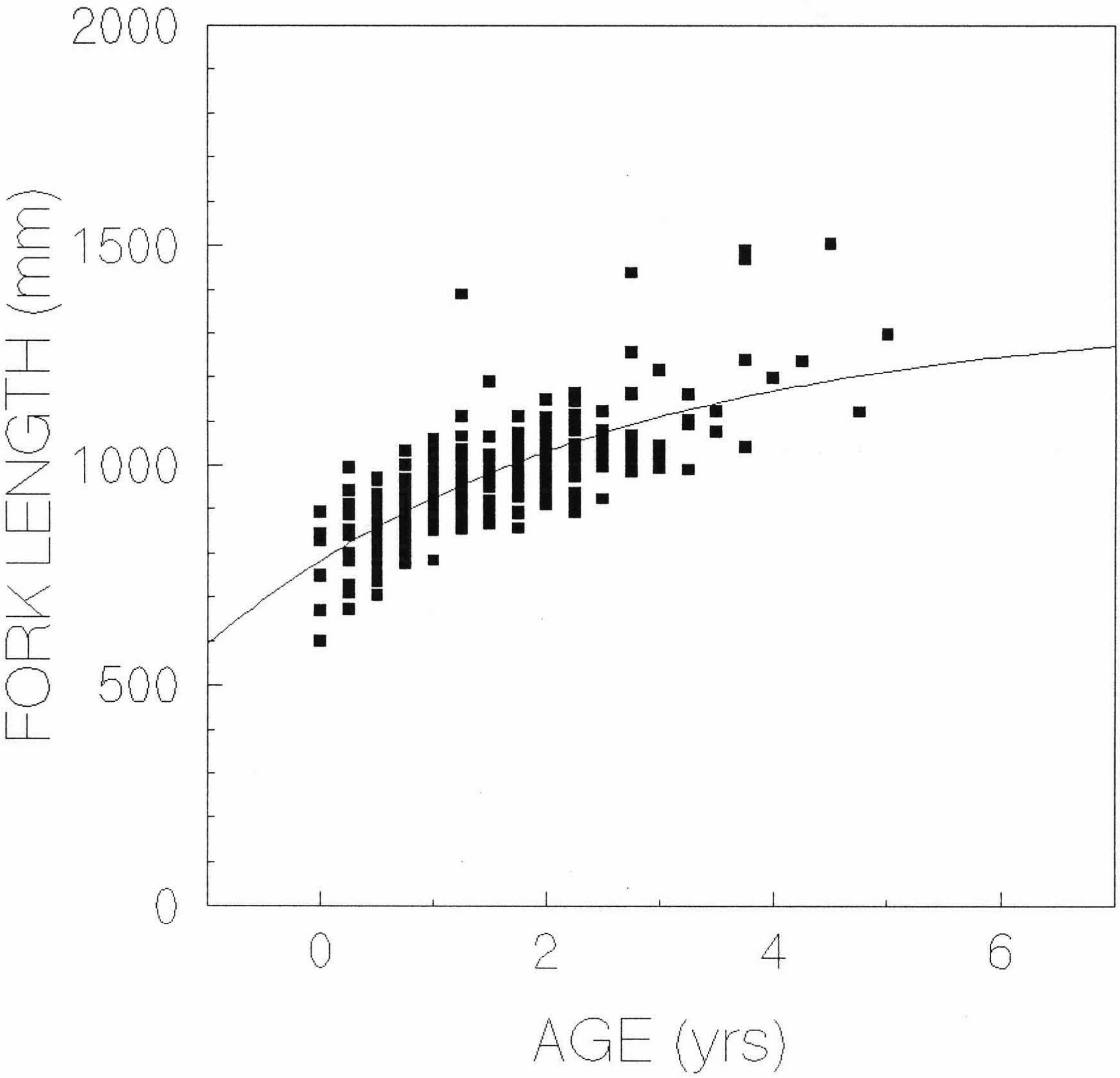

Figure 2 The relationship between length and age in *S. commerson*.

two tagged individuals was compared to those predicted by the fitted growth curves. The growth parameters that reasonably predict the observed values were selected as best and were used in all subsequent analyses. To predict time-at-liberty from the special Von Bertalanffy curve (equation 1) the following reformulation of equation 1 (which is usually used to estimate the special Von Bertalanffy parameters from mark-recapture data) was applied (Kirkwood, 1983):

$$\delta t = -\frac{1}{K}\ln\left(1 - \frac{\delta l}{L_\infty - R}\right) \qquad \textbf{(10)}$$

where δt is the time-at-liberty,

δl is the length increment between the time of tagging and recapture,

R is the length at tagging, and the other parameters are defined as in equation 1.

Table VIII summaries the parameter values of the special Von Bertalanffy equations used to estimate the time-at-liberty of the mark-recapture individuals.

Table VIII Summary of the special Von Bertalanffy growth parameter estimates (equation 1) derived in this study which are required to estimate time-at-liberty of tagged individuals using equation 10.

$\underline{L_{\infty}}$(mm)	K(yr^{-1})	METHOD	No. of opaque bands/year
1264	0.4699	length-based	-
1338	0.1479	age-based	ONE
1344	0.2918	age-based	TWO

Table IX summarises the observed and predicted time-at-liberty for the two tagged individuals as well as their mark-recapture length data. It is clear that the assumption of an annual opaque band being laid down in *S. commerson* leads to a gross underestimate of the growth rate (Table IX). Assuming biannual periodicity of the opaque band provides growth rates that follow closely the rates of tagged individuals (Table IX). The growth parameters derived from SLCA describe the growth rate of smaller fish (fish # 1) better than the larger individual (fish # 2, Table IX). This is to be expected since most of the growth information in length frequency distributions will be derived from younger cohorts which show greater separation of the mode classes. It is interesting to note that the SLCA derived growth parameters adequately describe the growth of *S. commerson* considering that length frequency distributions in this study show so little mode separation. However, the growth parameters assuming biannual periodicity of the opaque band describe better the time-at-liberty for fish # 2 (Table IX).

Table IX Observed and predicted time-at-liberty of two mark and recaptured *S. commerson*. M and R are the lengths at mark and recapture, respectively. * - indicates the annual periodicity of the opaque band assumed. $ - length estimated from the reported mass using the mass-fork length relationship.

Fish #	Fork length(mm)		Time Free(yrs)			
	M	R	Observed	Eq. 1 (one)*	Eq. 1 (two)*	Eq. 1 (SLCA)
1	710	940	1	3.08	1.54	1.14
2	900	1129.5$	2.8	5.02	2.49	2.12

As this individual falls within the peak exploited class range (900 to 1100mm), as compared to fish # 1 (Table IX), the parameters of the fitted curve assuming biannual periodicity of the opaque band were selected for all subsequent analyses.

4.4 SUMMARY AND CONCLUSIONS

The growth parameters derived from SLCA and those from the otolith study assuming biannual periodicity of the opaque band provided estimates that adequately describe the growth of young king mackerel (<1200mm). Both these growth curves also reasonable predicts the time-at-liberty for tagged individuals. Growth of young king mackerel is very rapid and this is consistent with the findings of other recent age studies on king mackerel (Dudley *et al.*, 1992; McPherson, 1992). It is probable that there are differences in the growth rates between sexes as suggested by the work of McPherson (1992). More research into this is needed.

CHAPTER FIVE

5. MORTALITY

5.1 Introduction

In an exploited fishery two aspects contribute to the decrease in biomass or numbers of fish: natural and fishing mortality. The latter is a result of the act of fishing. Assuming, in the population, that the rate of biomass increase (growth and recruitment) is lower than the rate of biomass decrease (mortality) of the population then, over the long term, fishing will explicitly reduce those age classes that are accessible and those that are vulnerable to the fishing gear (selectivity). These age classes are usually comprised of large fish, as they are most often sought by both sport fishermen (trophies) and commercial fishermen (bigger profits). It may also implicitly reduce the smaller inaccessible age classes, by reducing the spawning stock to a level that affects recruitment (assuming a spawner-recruit relationship exists at this level of fishing). Such effects may lead to the collapse of the fishery. Natural mortality consists of all factors, other than fishing which contribute to a decrease in population size (predation, disease, abiotic factors) and it is one of the most elusive parameters to estimate (Gulland, 1988). In an attempt to obtain reasonable estimates of natural mortality various investigators have related natural mortality to growth parameters and other biological characteristics of the population (Pauly, 1980; Rikhter and Efanov, 1977).

From the above it is intuitive that a knowledge of the mortality of an exploited species is essential for proper and successful management. Estimates of natural and fishing mortalities are required in dynamic pool models and are usually expressed as instantaneous rates (Ricker, 1975), simply because of mathematical convenience, in that rates can be added or subtracted directly (Pauly, 1984). This chapter reports the mortality rates of *S. commerson*.

5.2 Materials and method

The data used in determining the mortality rate estimates of *S. commerson* are reported on in chapters 3 and 4. The instantaneous natural mortality rate (*M*) was estimated using Pauly's empirical equation:

$$log M = -0.0066 - 0.279 log L_{\infty} + 0.6543 log K + 0.463 log T \qquad \textbf{(1)}$$

which requires estimates of the Von Bertalanffy growth parameters (L_{∞},K) (Chapter 4) and the mean environmental temperature (T) of the range of the species (Pauly, 1980). The mean environmental temperature (T) was taken to be 25 °C and M was tested for sensitivity to changes in T. Note, in equation 1, that L_{∞} is total length in centimetres, hence, the L_{∞} estimate reported in Chapter 4 was converted to total length using the total length-fork length relationship (equation 5, Chapter 4) and then, converted to centimetres. An independent estimate of M was obtained from the Rikhter and Efanov equation:

$$M = \frac{1.521}{t_{\mathrm{m}}^{0.72}} - 0.155 \qquad \textbf{(2)}$$

which requires an estimate of the age-at-50%-maturity (t_{m}) (Rikhter and Efanov, 1977).

This was obtained by using the Von Bertalanffy growth parameters to estimate the age of the length-at-50%-maturity of female *S. commerson* (1101mm, Chapter 2).

The total instantaneous mortality rate (Z) was estimated by two different techniques. Firstly, from the slope of the descending limb of the catch curve, i.e. by regressing natural logarithm of age frequency against age to all fully recruited ages. The age corresponding to the top of the catch curve was assumed to be the age-at-50%-capture (t_c) (Butterworth *et al.* 1989; Ricker, 1975). Secondly, from the following equation (Butterworth *et al.* 1989):

$$Z = \ln[1 + \frac{1}{(a_m - a_f)}] \qquad \textbf{(3)}$$

where a_f = age of full recruitment, and

a_m = mean age of all fully recruited fish sampled, with approximate 95% confidence limits:

$$Z \pm 2\frac{Z}{\sqrt{N}} \qquad \textbf{(4)}$$

where N = the number of fully recruited fish sampled.

To construct the catch curve a normalised age-length key was prepared from the age-length data obtained from otolith reading (Chapter 4). The total length frequency data (Chapter 3) were then transformed into age frequencies using this key (Butterworth *et al.* 1989; Buxton, 1987). The sensitivity of Z to the choice of the age-of-full-recruitment (a_f) and the age-at-50%-capture (t_c) was tested for both methods.

Given an estimate of *Z* and *M*, the instantaneous fishing mortality rate (*F*) was obtained by subtraction ($F=Z-M$).

5.3 Results and discussion

Table I shows estimates of the instantaneous natural mortality rate (*M*) of *S. commerson* obtained from Pauly's and the Rikhter and Efanov equations. The Rikhter and Efanov equation provides an *M* estimate higher than that of Pauly's equation, over the range of temperatures examined. Pauly (1980) found the standard deviation of *Log M* in equation 1 to be 0.245, equivalent to an *M* range of one-third to three times the estimate of *M* i.e 0.16 to 1.44yr^{-1} if *M* is 0.48yr^{-1} (Table I)(Gulland, 1988). Assuming that $Z=0.75yr^{-1}$ (see below) and, if it is known with some certainty, one can then deduce that the instantaneous fishing mortality rate (*F*) cannot be greater than 0.59yr^{-1} (Gulland, 1988). As the *M* estimate varies widely over the temperature range and between estimation methods, the average *M* estimate (Table I) has been taken as the instantaneous natural mortality rate for *S. commerson*. It is probably reasonable to assume such a high natural mortality rate because the majority of fish captured are 3yrs and less (Table II). Although McPherson (1992) aged *S. commerson* to at least 10yrs the majority he aged were also $\leq$ 3yrs.

Table I Instantaneous natural mortality rate estimates for *S. commerson*. The input parameters to equations 1 and 2 were $L_\infty=149.7$ (TL,cm), $K=0.291747\ yr^{-1}$, $T=22,25,28$ °C and $t_m=2.9$yrs, respectively.

EQUATION	T(°C)	M(yr^{-1})
Pauly	22	0.45
Pauly	25	0.48
Pauly	28	0.51
Rikhter and Efanov	-	0.55
AVERAGE		0.5

Table II shows the data used to estimate *Z* from the catch curve (Figure 1) and from equation 3. For both methods, the value of *Z* is sensitive to the choice of age-of-full-recruitment (a_f) or to the age-at-50%-capture (t_c), and the *Z* estimates also differ markedly for each estimation technique (Table III). The catch curve *Z* estimate is probably overestimated, since it does not take into account emigration which results in a steeper regression slope. Equation 3 also does not take into account emigration but, because this equation only requires estimates of the age-at-full-recruitment (a_f) and the mean ages of the fully recruited fish (a_m), it is reasonable to assume that estimation of both these parameters are not affected to any great degree by emigration. This *Z* estimate may, therefore, be more appropriate for *S. commerson*. Furthermore, Butterworth *et al.* (1989) point out that equation 3 may provide better estimates of *Z* than the catch curve especially if numbers caught at any age in the catch curve regression are low eg. numbers-at-age for ages ≥ 3yrs are low (Table II). The level of precision associated with the *Z* estimates derived from equation 3 may be too high (Table III). The confidence intervals calculated (equation 4) are based on the assumption that variation in recruitment, fishing and natural mortality is small from year to year, which in reality may not be so (Butterworth *et al.* 1989).

Table II The age frequency data of both sexes of *S. commerson* obtained from transforming the total length frequency using the age-length key.

AGE(yrs)	AGE FREQUENCY
0.00	233
0.25	309
0.50	1030
0.75	391
1.00	616
1.25	630
1.50	206
1.75	412
2.00	256
2.25	351
2.50	142
2.75	121
3.00	60
3.25	52
3.50	27
3.75	57
4.00	17
4.25	32
4.50	0
4.75	17
5.00	32

This assumption appears to be violated because the 95% confidence ranges for the *Z* estimates of the two different a_f values do not overlap and the confidence intervals

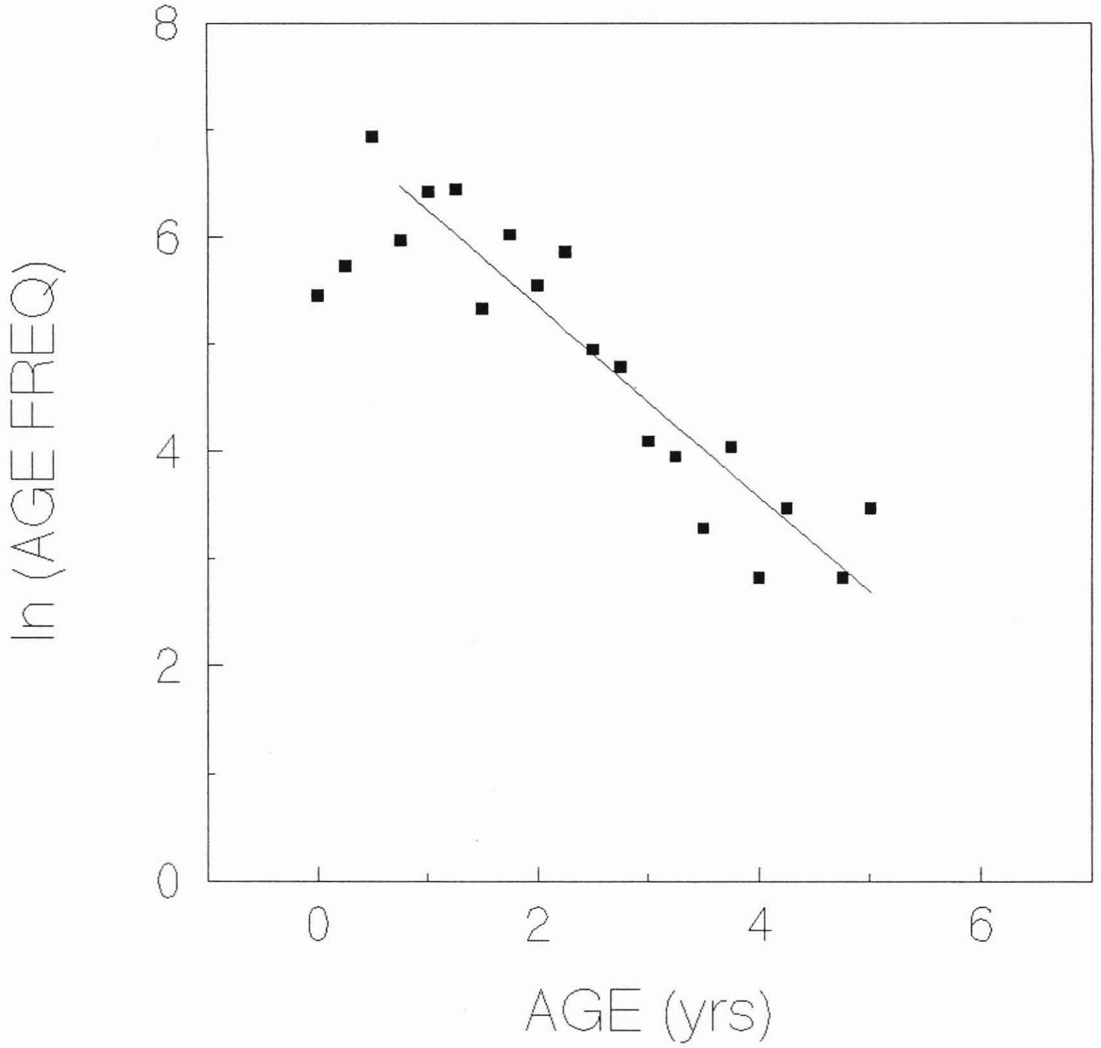

Figure 1 Catch curve of *S. commerson* showing the regression line fitted to the descending limb.

are much smaller than the difference between the *Z* estimates themselves (Table III). As it is uncertain which of the two techniques provides the most reasonable *Z* estimate, the average of both methods, when t_c and a_f are equal to 0.5yrs, was selected for *S. commerson*. This gives a *Z* estimate of $0.75yr^{-1}$.

Table III Total instantaneous mortality rate estimates for *S. commerson* with sensitivity tests to the choice of the age of full recruitment (a_f) and age-at-50% capture (t_c).

METHOD		$Z(yr^{-1})$	95% C.I.
ln(age freq) vs age	t_c=0.5yrs	0.89	±0.2
	t_c=0.75	0.94	±0.2
$Z=\ln[1+1/(a_m-a_f)]$	a_f=0.5yrs	0.61	±0.021
	a_f=0.75	0.66	±0.024

Therefore, from the equation $Z=F+M$ an estimate of *F* is $0.25yr^{-1}$ ($0.75-0.5yr^{-1}$). As the estimate of *F* is much smaller than the estimate of *M*, it would appear that the fishing pressure on *S. commerson* off the coast of Natal is not at a biologically critical level.

The estimates of the instantaneous fishing and natural mortality rates will be utilised in the yield-per-recruit model to assess the status of the Natal *S. commerson* fishery.

5.4 SUMMARY AND CONCLUSIONS

In this study *M* was estimated to be $0.5yr^{-1}$ which is well within the range of values assumed by Dudley *et al.* (1992) in their study of king mackerel (0.4 to $0.7yr^{-1}$). The current fishing mortality rate (*F*) was estimated to be $0.25yr^{-1}$ which is much smaller than *M*. This would indicate that fishing effort is not at a critically high level, at this stage. Further evidence, for such a belief, is that the total mortality rate (*Z*) of $0.75\mathrm{yr}^{-1}$ is probably overestimated (as a result *F* would be too) since the effects of emigration have not been taken into account. However, given that the mortality estimates vary between the methods applied more precise and independent estimates should be researched in the future.

CHAPTER SIX

6. YIELD-PER-RECRUIT AND SPAWNING BIOMASS-PER RECRUIT ANALYSIS

6.1 Introduction

Dynamic pool models, such as the Beverton and Holt yield-per-recruit model, relates the biomass of a year class of fish with time, following recruitment (Beverton and Holt, 1957). Under equilibrium conditions (mortality and growth rate, age-at-first capture and recruitment being constant over the fishable life of the year class) the yield from a single year class over its entire exploited life is equal to the yield from all year classes in any given year (Megrey and Wespestad, 1988). The biomass of the year class is simply the product of the numbers of and mean mass of the individuals in the year class (Butterworth *et al.* 1989) and it is reduced by both fishing and natural mortality. Unexploited year classes increase in biomass following recruitment because the growth rate generally exceeds the natural mortality rate at this time. The biomass then peaks and over time it would decline under natural mortality and a decreasing growth rate. This means that the shape of the yield curve is determined completely by the growth and mortality functions while recruitment determines only the magnitude of the yield realised (Megrey and Wespestad, 1988). The yield from a year class is determined by the age-at-first capture (t_c) and the fishing mortality rate (F) (Sissenwine and Shepherd, 1987).

The spawning biomass of the year class over its fishable life is the sum of the biomass at each age (B_i) times the proportion mature at each age (x_i), $\Sigma_i B_i x_i$ where *i* indexes the age classes (Sissenwine and Shepherd, 1987). The spawning biomass of a year class is also affected by the fishing mortality rate and the age-at-first capture with both decreasing the spawning biomass over time. Usually the yield and spawning biomass are normalised to the number of recruits entering the fishery since the level of recruitment is seldom known (Megrey and Wespestad, 1988).

A number of biological reference points are utilised in the yield-per-recruit (*Y/R*) and spawning biomass-per-recruit (*S/B*) analysis when assessing the current status of an exploited fishery or when recommending minimum size limits or target fishing mortalities (Sissenwine and Shepherd, 1987). F_{max} is the fishing mortality rate that maximises the yield-per-recruit. However, in some exploited stocks the yield curve is asymptotically shaped, eg. in species that have a low growth and high natural mortality rate (Megrey and Wespestad, 1988). In these cases there is no obvious F_{max} point on the yield curve. As an alternative $F_{0.1}$ has been proposed since it produces as much yield as F_{max} without reducing the spawning biomass as severely (Sissenwine and Shepherd, 1987). $F_{0.1}$ is defined as that fishing mortality rate that corresponds to a point on the yield-per-recruit curve where the slope is 10% of that at the origin (Gulland and Boerema, 1973). In the case of the spawning biomass-per-recruit curve there are no corresponding biological reference points that are defined. However, Butterworth *et al.* (1989) recommend maintaining a fishing mortality rate close to the rate at which the spawning stock is reduced to 50% of its average unexploited level (F_{SB50}). Clark (1991) recommends for groundfish that maintaining a spawning biomass at 35% of its unfished level will provide high yields at low risk even if no knowledge of the yield curve or spawner-recruit relationship is known. In this study the fishing mortality corresponding to this spawning biomass will be designated as F_{SB35}.

This chapter summarises the yield-per-recruit and spawning biomass-per-recruit analyses conducted, to determine the optimum fishing mortality rate and age-at-first capture (minimum size limit) for *S. commerson*, such that there is a reasonable trade-off between maximising yield-per-recruit and maintaining the spawning biomass-per-recruit at a sound biological level.

6.2 Materials and methods

The yield-per-recruit (*Y/R*) and spawning biomass-per-recruit (*S/R*) analyses were performed on three different growth curves (chapter 5) for *S. commerson* and were computed from the following integral equations, respectively (Punt, 1992):

$$Y/R = \int_0^{\infty} S_t . F . \frac{N_t}{N_0} . W_t . dt \qquad \textbf{(1)}$$

where

S_t = the selectivity of the fishing gear on fish age t yrs. In this analysis selectivity has been assumed to be knife-edged i.e.

$$S_t = \begin{cases} 0 & \text{if } t < t_c \\ 1 & \text{if } t \geq t_c \end{cases} \qquad \textbf{(2)}$$

where t_c is the age-at-50%-capture and was assumed to be represented by the age corresponding to the top of the catch curve (chapter 5),

F = the instantaneous fishing mortality rate on fully recruited year classes,

N_t = the number of t year old fish in the population,

W_t = the mean mass of a t age fish.

$$S/R = \int_0^{\infty} \beta_t . \frac{N_t}{N_0} . W_t . dt \qquad \textbf{(3)}$$

where

β_t = the proportion of mature fish at age t and the other parameters are defined as in equation 1.

For the per-recruit analysis an estimate of the age-at-50%-maturity (t_m) is also required (Punt, 1992). This was obtained by converting the length-at-50%-maturity for female king mackerel to an age using the appropriate growth curves (chapter 5). Maturity was also assumed to be a knife-edge process. The software PC-YIELD was used to generate the per-recruit curves and to estimate $F_{0.1}$ and F_{SB50} (Punt, 1992). The fishing mortality (F_{SB35}) at which the spawning biomass is reduced to 35% of its unfished level was estimated graphically. Various ages-at-first-capture were examined in the per-recruit analyses.

6.3 Results and discussion

Table I summaries the biological and technological parameters utilised in the per-recruit analyses. The t_c and t_m values are based on the length-at-50%-capture for both sexes (860mm) and length-at-50%-maturity (1096mm) for female *S. commerson*, respectively and were converted to age estimates using the appropriate growth curves (Table I).

Table I Biological and technological parameter values utilised in the per-recruit analyses for *S. commerson*. In the acronym VONB X, VONB indicates that the Von Bertalanffy growth function was fitted to the age-length data and X indicates the annual periodicity of the opaque band assumed.

PARAMETER	SLCA	VONB 1	VONB 2
L_∞ (mm)	1264	1338	1344
K (yr^{-1})	0.470	0.148	0.292
t_0 (yrs)	-0.877	-5.957	-2.999
M (yr^{-1})	0.5	0.5	0.5
F (yr^{-1})	0.25	0.25	0.25
t_c (yrs)	1.6	1.0	0.5
t_m (yrs)	3.4	5.6	2.8
a	0.1353×10^{-5}	0.1353×10^{-5}	0.1353×10^{-5}
b	3.2515	3.2515	3.2515

Figure 1 shows the yield- and spawning biomass-per-recruit curves for three different growth functions of *S. commerson*. Table II shows some management and biological reference points relative to these per-recruit curves. For all three growth curves the yield-per-recruit increases with increased fishing (Figure 1b). Surprisingly the SLCA and VONB 1 yield-per-recruit curves are almost identical (Figure 1b).

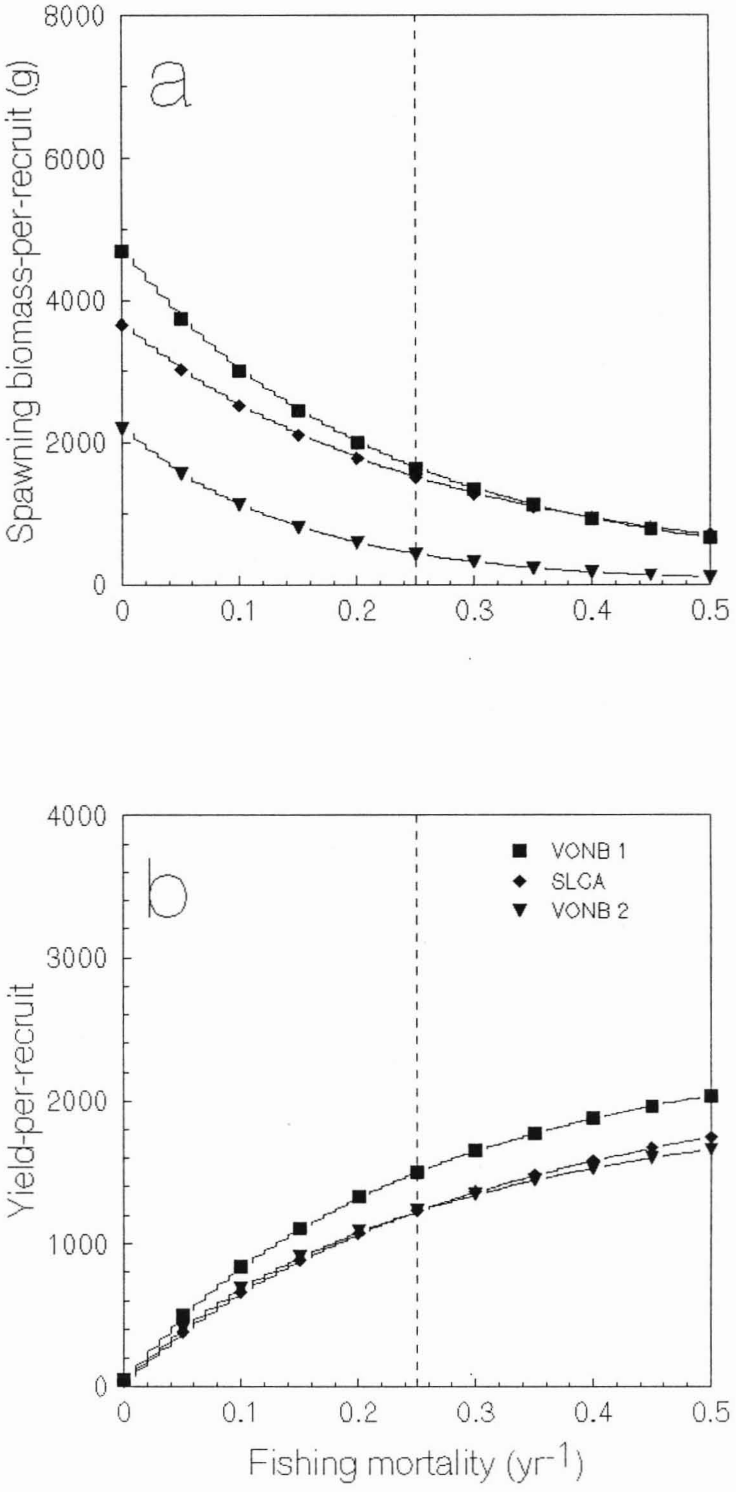

Figure 1 Spawning biomass-per-recruit (a) and yield-per-recruit (b) curves of *S. commerson* for input parameter values shown in Table I. Dashed line indicates the current fishing mortality rate.

Table II Target management fishing mortality rates for *S. commerson*. See text for definitions.

PARAMETER(yr^{-1})	SLCA	VONB 1	VONB 2
F_{max}	5.8	5.0	∞
$F_{0.1}$	0.8	0.6	0.6
F_{SB50}	0.19	0.10	0.16
F_{SB35}	0.32	0.17	0.26

However, they differ markedly in their spawning biomass-per-recruit curves. The VONB 1 spawner biomass-per-recruit curve displays the lowest spawning biomass-per-recruit values per fishing rate (Figure 1a). For this growth curve the spawning biomass drops to 50 and 35% of the unexploited level at fishing mortalities much lower than the current fishing mortality rate (F=0.5 yr^{-1})(Table II). This is a result of the relative slow somatic growth rate, early age-at-first-capture and late age-at-maturity predicted by the VONB 1 growth curve (Table I,II). In fact, at $F = M = 0.5$ yr^{-1}, the VONB 1 growth curve predicts a virtual collapse of the fishery (Figure 1a). However, maintaining $F=M$ is a common management strategy which is based on the belief that maximum sustainable yield is obtained at these rates (Clark, 1991). Currently, *F* is half *M* and at this fishing rate the VONB 1 growth function indicates that the current spawning biomass-per-recruit is approximately 20% of the unfished level (Figure 1a). Even at a low fishing mortality rate of 0.1 yr^{-1}, which is 83% lower than $F_{0.1}$ (Table II), the VONB 1 growth curve predicts that the spawning biomass will be 50% of the unexploited level (Table II). Considering that the above scenario predicted by the VONB 1 growth curve is unrealistic for the Natal *S. commerson* fishery and further that the VONB 1 growth curve grossly underestimates the growth rate of *S. commerson* (chapter 5) no further per-recruit analyses are conducted for this growth curve.

For all growth curves the maximum yield-per-recruit is reached at infinite fishing mortality or at very large fishing mortality rates (Table II, Figure 1a). From a pristine level to approximately 0.2 yr^{-1} fishing mortality, the VONB 2 growth function indicates a greater spawning biomass-per-recruit than the SLCA growth function (Figure 1a). However, between fishing mortalities 0.2 and 0.3 yr^{-1} the VONB 2 curve indicates only marginally higher spawning biomass-per-recruit than the SLCA curve (Figure 1a). Beyond a fishing mortality of 0.3 yr^{-1} the spawning biomass-per-recruit are identical for both growth curves (Figure 1a). However, within these same fishing mortality ranges the yield-per-recruit realised from the VONB 2 growth curve is higher than that of SLCA (Figure 1b).

The SLCA and VONB 2 growth curves predict that the spawning biomass-per-recruit is currently at 42 and 35% of the unfished level, respectively (Figure 1a, Table II). Considering that the current fishing mortality rate is positively biased (because it includes an emigration factor) these percentage estimates may be too low.

Table III indicates the potential benefits that can be realised for three different minimum size limits. These minimum sizes correspond to the length-at-50%-maturity for female *S. commerson* and its upper and lower 95% estimates.

Table III. Biological reference points for *S. commerson* for three different minimum size limits.

MINIMUM SIZE (mm)	MANAGEMENT VARIABLE (yr^{-1})	SLCA	VONB 2
1034 (lower 95%)	*F*max	7.10	∞
	$F_{0.1}$	0.91	0.78
	F_{SB50}	0.31	0.26
	F_{SB35}	0.45	0.42
1096 (length-at-50%-maturity)	F_{max}	7.39	6.67
	$F_{0.1}$	0.94	0.83
	F_{SB50}	0.46	0.41
	F_{SB35}	$\approx$0.6	$\approx$0.6
1158 (upper 95%)	F_{max}	∞	∞
	$F_{0.1}$	1.02	0.9
	F_{SB50}	1.73	1.25
	F_{SB35}	$>$1	$>$1

Figures 2 and 3 illustrate the per-recruit analyses based on these minimum sizes for the growth curves VONB 2 and SLCA, respectively. As can be seen there is very little difference in the per-recruit trajectory shapes for these growth curves (Figure 2,3). Generally, it can be shown that by increasing the size/age-at-first-capture yield-per-recruit decreases with a corresponding increase in spawning biomass-per-recruit (Figure 2,3). The magnitude of increase or decrease is dependent on the age-at-first-capture and the current mortality rate. Per-recruit analyses were also conducted for an age-at-first-capture of 1 yr for the VONB 2 growth curve. However, only marginal changes in the yield-per-recruit and spawning biomass-per-recruit were observed as compared to the current age-at-first-capture of 0.5 yrs. Biological reference point values for these growth curves, for the same size-at-capture, are very similar (Table III). Note that $F_{0.1}$, for all three minimum sizes, are very similar for each growth curve. However, the F_{SB50} and F_{SB35} values are quite different (Table III). This suggests that the three minimum size limits will roughly maximise the yield-per-recruit at the same fishing effort. However, conservation of the spawning biomass-per-recruit increases

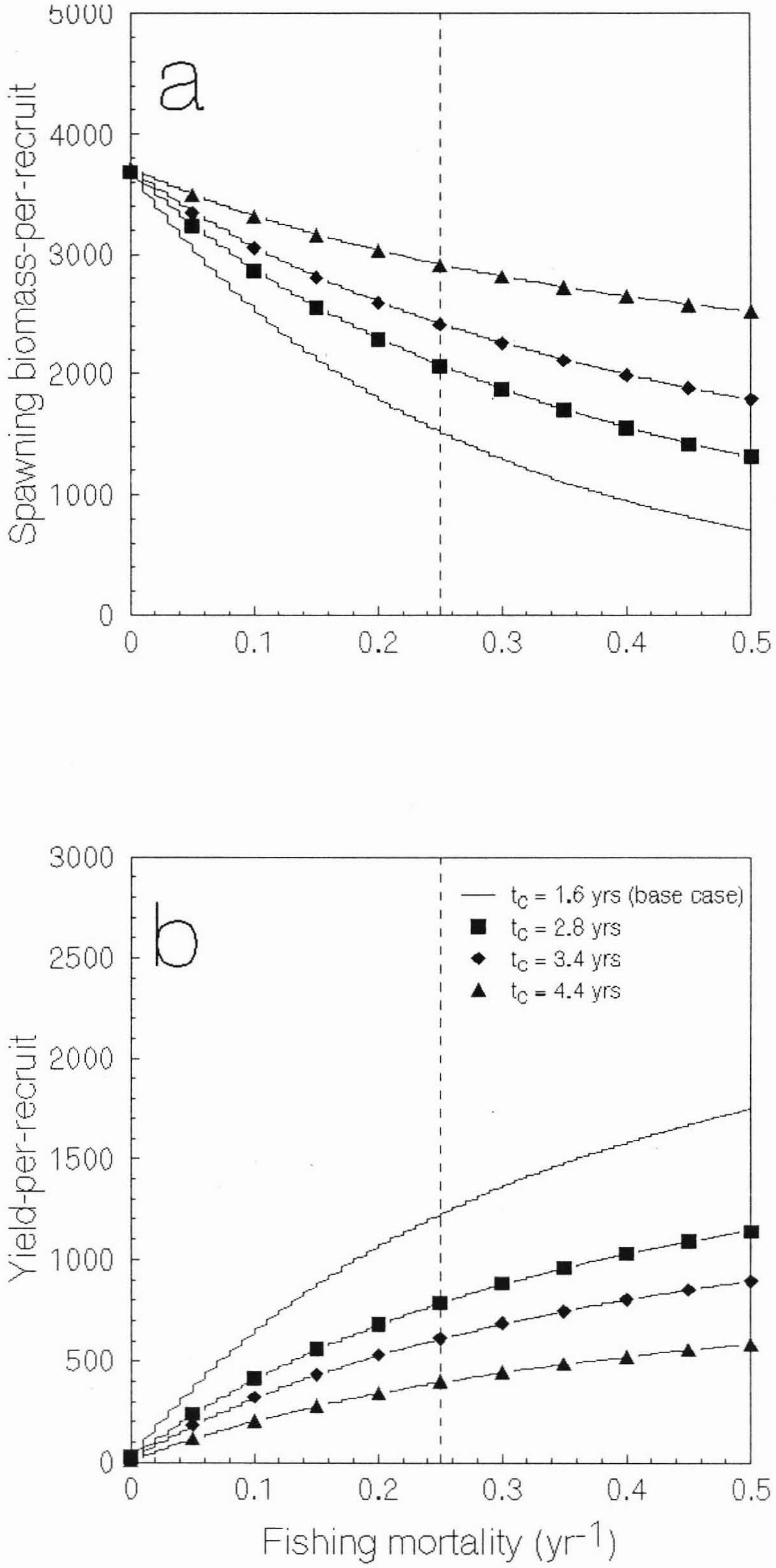

Figure 2 Spawning biomass-per-recruit (a) and yield-per-recruit (b) based on the growth curve SLCA for three different minimum sizes for *S. commerson*. Dashed line indicates the current fishing mortality.

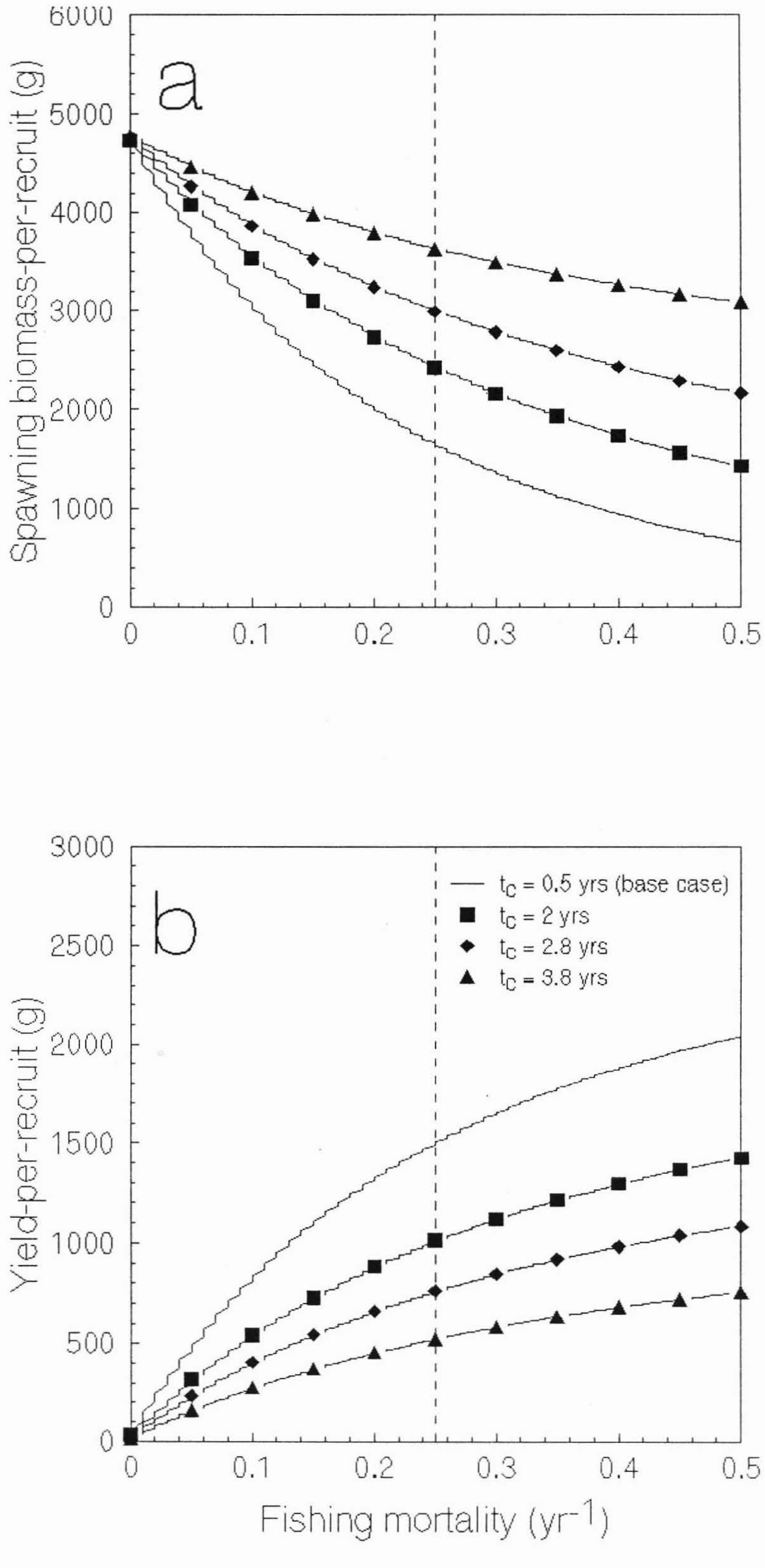

Figure 3 Spawning biomass-per-recruit (a) and yield-per-recruit (b) based on the growth curve VONB 2 for three different minimum sizes for *S. commerson*. Dashed line shows the current fishing mortality.

with an increase in size-at-capture.

6.4 SUMMARY AND CONCLUSIONS

The yield-per-recruit and spawning biomass-per-recruit analysis indicate that the per-recruit estimates are sensitive to the choice of growth parameters. For example, the growth curve assuming annual periodicity of the opaque band (VONB 1) predicts a virtual collapse of the fishery when $F = M$. At the current age-at-first-capture it also predicts that the spawning biomass will be 50% of its unexploited level at a low fishing mortality rate of 0.1yr^{-1}. This sceanario is considered unrealistic for the Natal king mackerel fishery. The per-recruit analyses based on the other two growth curves (SLCA and VONB 2) indicate that the fishery is healthy with no evidence of biological overexploitation. The current spawning biomass is probably at a minimum value of 35% of its unfished level. However, this percentage in reality may be low because the current estimate of F is positively biased. Setting a minimum size above the length-at-maturity, for female king mackerel, will result in short term deceases in yield but with substantial gains in spawning biomass-per-recruit. However, if differential growth occurs between the sexes, which is probable, then the per-recruit assessment needs to be re-evaluated.

CHAPTER SEVEN

7. IMPLICATIONS FOR MANAGEMENT

In an open access fishery such as the recreational king mackerel fishery of Natal, managment options such as minimum size or bag limits, closed seasons or areas are usually implemented to reduce fishing effort. Usually a combination of these restrictions are implemented. Currently the only restrictions on king mackerel are a bag limit on recreational catches while commercial fishermen have limited entry but no restrictions on catches. As king mackerel is a coastal migrant and abundance is seasonally related it is not realistic to implement closed seasons or areas in Natal. The only other management option other than current bag limits is a minimum size limit. This will protect the spawning stock, if fishing pressure on this species continues to increase.

Although in principle setting a minimum size such as a length above the length-at-50%-maturity will offer a refuge for immature and first spawning individuals, in practice, this may not be feasible because of the socio-economic implications of such a management strategy. Setting a minimum size equal to the size-at-50%-maturity for king mackerel may substantially reduce catches in the short and medium term because at least 90% of the catch currently being taken will be inaccessible to fishing (Figure 1). Furthermore, this minimum size is well above the current mean catch size of both sexes (934mm). Additionally, such a size limit will offer greater protection to males rather than females. This will result in a skewed catch sex ratio. An equally important consideration is that a minimum size implemented in Natal may not only benefit local fishermen but also those in Mozambique due to the coastal migratory nature of *S. commerson*. Local fishermen would perceive that substantial sacrifices are being made unilaterally. Nevertheless, at present, this is not an important consideration since Natal fishermen harvest more king mackerel than neighbouring countries. However, the situation may change if there is renewed and intensified fishing in Mozambique. Therefore, any management strategy adopted should be acceptable and enforced both in Natal and Mozambique.

It is believed that the current restrictions on sport catches of 10 king mackerel/person/day offers adequate protection for the Natal king mackerel stock. However, if fishing effort on this species continues to increase, as is anticipated in this open access fishery, or if there is increased commercial interest or if there is renewed fishing in Mozambique, some fishing effort restrictions may be necessary to protect the spawning stock. In this case, it may be prudent, that a minimum size corresponding to the lower 95% confidence estimate of the size-at-50%-maturity (1034mm,FL) be considered. Such a management strategy may be acceptable to recreational anglers because some recreational anglers have called for a minimum size limit (Winch, 1990) and secondly king mackerel is mainly targeted by recreational skiboat anglers. Furthermore, sport fishermen pursue king mackerel for its trophy value as well as its fighting potential. Both these characteristics may be enhanced by a minimum size as large king mackerel will now be targeted. However, this management strategy will certainly have negative socio-economic effects on commercial fishermen because at least 90% of the catch currently taken in Natal will be inaccessible to them (Figure 1).

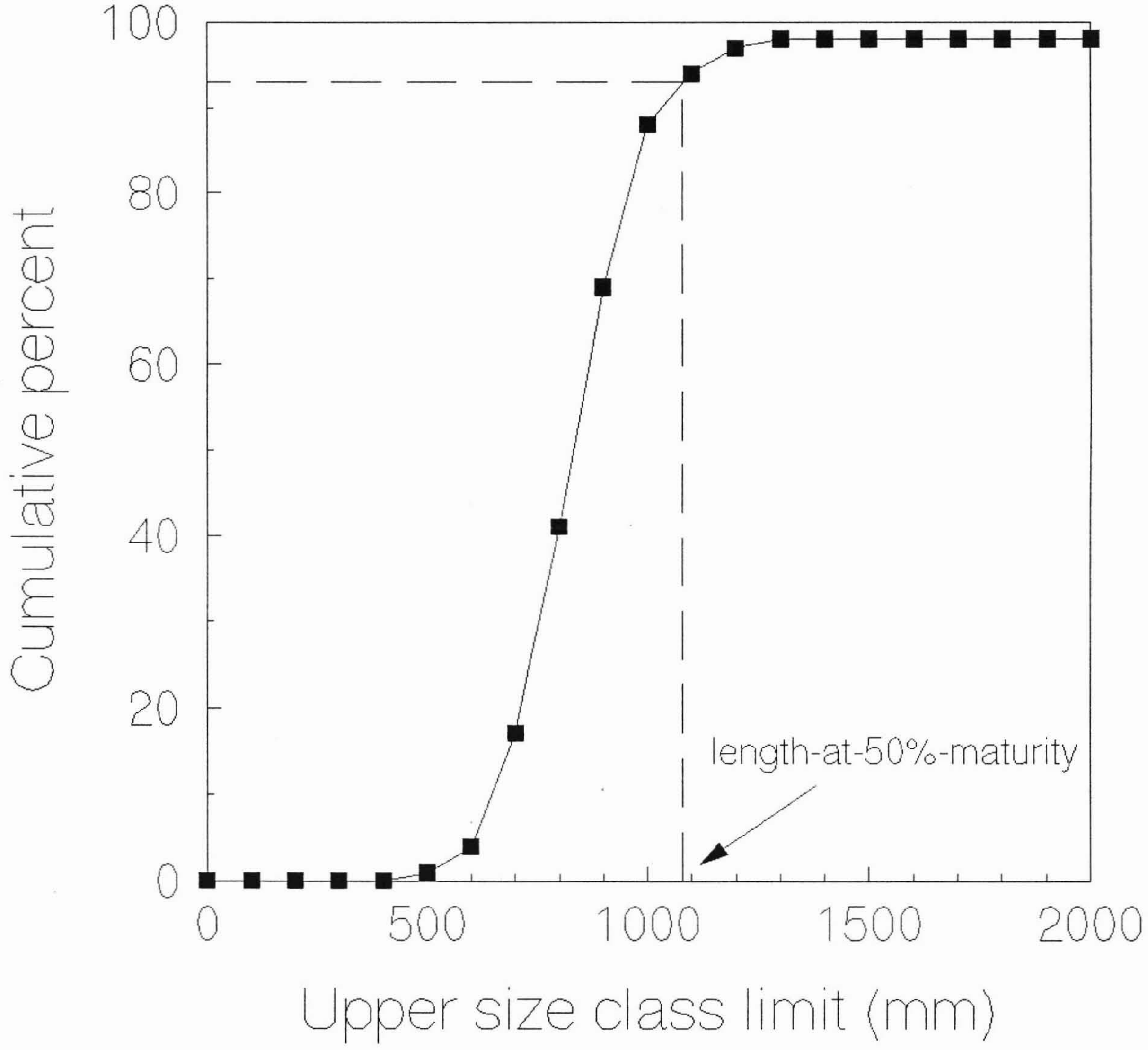

Figure 1 Cumulative percentage frequency of catches of *S. commerson*.

Although commercial fishermen largely direct their fishing effort to "redfish", king mackerel, nevertheless, forms an important part of their total catch especially to those fishing on the north coast of Natal. A minimum size strategy, if implemented and enforced only in Natal, may still not be beneficial as Natal's commercial fishermen may simply turn to Mozambican waters.

Arguably, if the annual migration of king mackerel to Natal waters is simply a post-spawning, feeding migration (61% of mature females captured in Natal are in post-spawning condition) then a minimum size to protect the spawning stock should, in all practicality, be implemented in Mozambique, the principal spawning area for *S. commerson*. Furthermore, the minimum size selected should be based on maturity data collected from this area. No other restrictions other than current restrictions should thus be implemented in Natal.

What effect such measures have on the current fishery in Mozambique, eg. the artisanal fishery, cannot be assessed as very little is known of catches taken there. It is believed that the aforementioned strategy is the most reasonable management option which will offer some protection to the spawning stock. Such a joint and international agreement has political implications that go beyond a mere comment from science.

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GLOSSARY

The following is a list of mathematical symbols and their definitions which are found in this thesis.

β_t	the proportion of mature fish at age t
δ	parameter that determines the width of the maturity ogive
δl	length increment between the time of tagging and time at recapture
δt	time-at-liberty for a tagged fish
a	mass-length parameter
a, b	Schnute growth model parameters that determine the shape of the growth curve
a_f	age of full recruitment
a_m	mean age of all fully recruited fish sampled
b	mass-length parameter
F	instantaneous fishing mortality rate
$F_{0.1}$	fishing mortality rate that corresponds to a point on the yield-per-recruit curve where the slope is 10% of that at origin
FL_i	fork length of i'th fish
F_{max}	fishing mortality rate that maximises the yield-per-recruit
F_{SB35}	fishing mortality rate at which the spawning stock is reduced to 35% of its average unexploited level
F_{SB50}	fishing mortality rate at which the spawning stock is reduced to 50% of its average unexploited level

K	rate at which L_t approaches the asymptote
L_i	length of i'th fish
L_t	length at age t,
L_∞	mean asymptotic length,
M	instantaneous fishing mortality rate
ML_i	maxillary length of the i'th fish
Q	the difference between t_{max} and t_{min}
R_i	length at tagging of the i'th fish
S_t	the selectivity of the fishing gear on fish age t yrs. In this analysis selectivity has been assumed to be knife-edged
T	mean environmental temperature
t_0	length at "zero" length.
t_a	average age of t_{max} and t_{min}
t_c	age-at-50%-capture
TL_i	total length of the i'th fish
t_m	age-at-50%-maturity
t_{max}	Von Bertalanffy age that corresponds to upper bound of length class L
t_{min}	Von Bertalanffy age that corresponds to lower bound of length class L
t_s	fraction of the annual cycle when sample was taken
W_i	mass of i'th fish
$X_{0.5}$	length-at-50%-maturity
X_{mid}	midpoint of the class interval X
Y	proportion of mature fish in length class X
y_1, y_2	sizes in the Schnute growth model that corresponds to two ages T_1 and

	T_2 (such as the youngest and oldest observed ages), respectively
Z	total instantaneous mortality rate

APPENDIX [A.1]

TITLE: SLCAI

REFERENCES: (Shepherd, 1987; Holden and Bravington, 1992)

LANGUAGE: Turbo Pascal Version 5.5

HARDWARE REQUIRED: IBM compatible computer, Printer

OPERATING SYSTEM: MS DOS Ver 3.3 or higher

DESCRIPTION: The program SLCAI indicates which Von Bertalanffy growth parameters best describe the growth information in length frequency data. This is performed by fitting Von Bertalanffy growth curves to the modes and troughs in a time series of length frequency data. A test function is constructed from the range of growth parameter estimates which is input by the investigator. A goodness of fit criterion, which is similar to a correlation coefficient between the data and the test function is then used to select the parameters which best describes the data.

PROGRAM LISTING:

```
{WRITTEN BY A. GOVENDER SEPT. 1991}
{Function subroutine ATAN2 written by A.E. Punt, UCT}
{This program given a set of length frequency data will estimate}
{the von Bertalannfy parameters}
```

```
{REFERENCE:A weakly parametric method for estimating growth}
{parameters from length composition data by J.G.Shepherd.}
{In:Length-based methods in fisheries}
{research-Pauly,Morgan(editors). See also}
{Shepherds program at the end of the book}
{warning: program under development}

PROGRAM slcai;

USES crt,printer;

VAR
        ts:ARRAY[1..12] of REAL;
        leng:ARRAY[1..50] of REAL;
        num:ARRAY[1..50,1..12] of REAL;
        linf:ARRAY[1..11] of REAL;
        tzero:ARRAY[1..2] of REAL;
        k:ARRAY[1..11] of REAL;
        score:ARRAY[1..11,1..11] of REAL;
        tmin:ARRAY[1..51] of REAL;
        tmax:REAL;
        tscore:ARRAY[1..2] of REAL;
        tz:ARRAY[1..11,1..11] of REAL;
        lmin,kk,inc,llinf:REAL;
        id,nlzero,ilzero,ilinf: INTEGER;
        ik,nk,nlinf,i,l,ndist,nl: INTEGER;
        ttz,phi,a,b:REAL;
        ch:CHAR;
        fil:STRING;
        inp:TEXT;
        key:BOOLEAN;
        title:STRING[20];

(*************************************************************)
FUNCTION sum (kk,llinf,tzero:REAL):REAL;

VAR

  tmin:ARRAY[1..51] of REAL;
  diffn,tbar,deltas,delt,tmax,rk:REAL;
  sum1:real;
  llzero:real;
  discr:ARRAY[1..12] OF REAL;

BEGIN {function}

    rk:=1/kk;                    {inverse of k-value}
    llzero:=llinf*(1-EXP(kk*tzero)); {length at t0=0;0.25}
```

```
     sum1:=0;                { set score to zero}
  {*******calculate ages for lower limits of length classes*****}
     FOR l:=1 TO (nl +1) DO  {loop 400}
         BEGIN
              IF leng[l] < llinf THEN key:=TRUE ELSE key:=FALSE;
                  IF key THEN
                    BEGIN
                  tmin[l]:=rk*(LN((llinf-llzero)/(llinf-leng[l])));

                    END{if};
         END; { 400}
   FOR l:=1 TO nl DO  {loop 600}
      BEGIN
    IF leng[l+1] < llinf THEN key:=TRUE ELSE key:=FALSE;
       IF key THEN
         BEGIN
     tmax:=tmin[l+1]; {ages at upper limits of length classes}
     delt:=tmax-tmin[l];  {diff. bet. ages}
     tbar:=0.5*(tmax+tmin[l]);   {average age}
     diffn:=SIN(PI*delt)/(PI*delt);

                 FOR id:=1 TO ndist DO  {loop 700}
                  BEGIN
                   discr[id]:=diffn*(COS(2*PI*(tbar-ts[id])));
                   deltas:=(SQRT(num[l,id]))*discr[id];
                   sum1:=sum1 + deltas;
                   sum:=sum1;
                  END; {700}
             END;{if};
     end{600};
   end{function};
(***************************************************************)
FUNCTION ATAN2(b,a:REAL):REAL;
(* FORTRAN-like ATAN2 *)

BEGIN
  IF (b > 0) THEN
   BEGIN
    IF (a > 0) THEN
      ATAN2 := ARCTAN(b/a)
    ELSE
      ATAN2 := PI - ARCTAN(ABS(b/a));
   END
 ELSE
   BEGIN
    IF (a > 0) THEN
      ATAN2 := ARCTAN(b/a)
    ELSE
```

```
      ATAN2 := ARCTAN(ABS(b/a)) + PI;
   END;
END;
(**************************************************************)
BEGIN {program}
   CLRSCR;
     WRITELN('ENTER NAME OF FILE TO PROCESS');
     READLN(fil);
     ASSIGN(inp,fil);
     RESET(inp);

WHILE NOT (EOF(inp)) DO
 BEGIN {reading from data file}
   BEGIN
 {lmin=lower limit of smallest leng. class;nl=no. of leng. class}
         {inc=leng.class increment;ndist=no.of seasons}
           READLN(inp,lmin,nl,inc,ndist);
    END;
               FOR i:=1 TO ndist DO
                BEGIN
                   READ(inp,ts[i]);{read fraction of seasons}
                END;
       FOR l:=1 TO nl DO {loop 810}
     BEGIN
       READ(inp,leng[l]); {read lower limits of leng.classes}
                      FOR i:=1 TO ndist DO
                      BEGIN
                       READ(inp,num[l,i]); {read nums. at leng.}
                    END;
                END; {810}
         leng[nl+1]:=leng[nl]+inc;{leng.upper bound}
(**************************************************************)
     CLRSCR;
     WRITELN('SHEPHERDS LENGTH COMPOSITION ANALYSIS');
     LOWVIDEO;
     WRITE('e');
     HIGHVIDEO;
     WRITE('X');
     LOWVIDEO;
     WRITELN('plore for various K"s and Linf"s ?');
     ch:=READKEY;
     IF ch IN ['X','x'] THEN key:= TRUE ELSE key:=FALSE;
      IF key THEN
           BEGIN
             WRITELN('ENTER SPECIES NAME');
             READLN(title);
             WRITELN('NO. OF VALUES FOR L-INFINITY');
             READLN(nlinf);
```

```
     IF (NOT(key)) THEN HALT;
      WRITELN('ENTER L-INFINITY VALUES');

            FOR i:=1 TO nlinf DO
                BEGIN
                    READLN(linf[i]);
                END;
       CLRSCR;
(***********************************************************)
    nlzero:=2;
     FOR i:=1 TO nlzero DO {100}
      BEGIN {100}
           tzero[i]:=0.25*(i-1); {set t0 to 0 and 0.25}
      END; {100}
(************************************************************)
 IF ch IN ['X','x'] THEN key:=TRUE ELSE key:=FALSE;
   IF key THEN
         BEGIN
           WRITELN('ENTER NO. OF K-VALUES');
           READLN(nk);
         END;{if}

      WRITELN('ENTER K-VALUES');
      FOR i:= 1 TO nk DO
          BEGIN
           READLN(k[i]);
          END;
      WRITELN('PLEASE WAIT');
 (***********************************************************)
    IF CH IN ['X','x'] THEN key:=TRUE ELSE key:= FALSE;
       IF key THEN
          BEGIN
             FOR ilinf:=1 TO nlinf DO {loop 200}
                   BEGIN
                        llinf:=linf[ilinf];
               FOR ik:=1 TO nk DO {loop 300}
                   BEGIN
                        kk:=k[ik];

   FOR ilzero :=1 TO nlzero DO{loop 500}
   BEGIN
    tscore[ilzero]:= sum(kk,llinf,tzero[ilzero]);{compute scores}
   END{500};

    a:=tscore[1]; {set score when t0=0}
    b:=tscore[2]; {set score when t0=0.25}
    score[ilinf,ik]:=SQRT(a*a+b*b); {store max. scores}
    phi:= ATAN2(b,a);
```

```
  ttz:=(phi/(2*PI)); {compute t0 for max. score}
    IF ttz < 0 THEN  ttz:=ttz+1;
  tz[ilinf,ik]:=ttz;        {store t0 values}

 END{300};
END{200};
(****************************************************************)
     CLRSCR;
     WRITELN(LST,'LENGTH COMPOSITION ANALYSIS BY SLCA FOR');
     WRITELN(LST,title);
     WRITELN(LST,'TABLE OF SCORE FUNCTION');
     WRITELN(LST,'                    ','VALUE OF K');
     WRITE(LST,'    LINF');
          FOR ik:=1 TO nk DO
            BEGIN
              WRITE(LST,k[ik]:8:2);
            END;
          WRITELN(LST,' ');
       FOR ilinf:=1 TO nlinf DO{loop 801}
             BEGIN
               WRITE(LST,linf[ilinf]:8:2);
          FOR ik:=1 TO nk DO
               BEGIN
                 WRITE(LST,score[ilinf,ik]:8:1);
               END;
             WRITELN(LST,' ');
            END;{801}

     WRITELN(LST,' ');
     WRITELN(LST,'TABLE OF T-ZERO');
     WRITELN(LST,'                    ','VALUE OF K');
     WRITE(LST,'    LINF');

        FOR ik:=1 TO nk DO
           BEGIN
               WRITE(LST,k[ik]:8:2);
           END;
              WRITELN(lST,' ');
        FOR ilinf:=1 TO nlinf DO{loop 800}
              BEGIN
                WRITE(LST,linf[ilinf]:8:2);
                   FOR ik:=1 TO nk DO
                       BEGIN
                         WRITE(LST,tz[ilinf,ik]:8:1);
                       END;
                WRITELN(LST,' ');
           END;{800}
     END;{IF}
```

```
    END;
  END;
END.
```

APPENDIX [A.2]

TITLE: SLCAII

REFERENCES: (Shepherd, 1987; Holden and Bravington, 1992)

LANGUAGE: Turbo Pascal Version 5.5

HARDWARE REQUIRED: IBM compatible computer, Printer

OPERATING SYSTEM: MS DOS Ver 3.3 or higher

DESCRIPTION: The program SLCAII, given a set of Von Bertalanffy growth parameters such as that derived from SLCAI will calculate the ages of the class limits in the length frequency data and then score them using score calculations as in SLCAI.

PROGRAM LISTING:

```
{WRITTEN BY A. GOVENDER SEPT 1991}
{This program given a set of von Bertalannfy parameters derived}
{from the program slcai and the length frequency data will}
{determine the age of the lower limits of the length groups and}
{score them.}
{REFERENCE: A weakly parametric method for estimating growth}
{parameters from length composition data by J.G. Shepherd. IN:}
{Length-based methods in fisheries}
{research.Pauly,Morgan(editors).See also Shepherds program at}
{the end of the book}
```

```
{warning:program under development}

PROGRAM slcaii;

USES crt,printer;

VAR
        discr:ARRAY[1..12] of REAL;
        ts:ARRAY[1..12] of REAL;
        leng:ARRAY[1..50] of REAL;
        num:ARRAY[1..50,1..12] of REAL;
        linf:ARRAY[1..11] of REAL;
        k:ARRAY[1..11] of REAL;
        score:ARRAY[1..11,1..11] of REAL;
        tmin:ARRAY[1..51] of REAL;
        numa:ARRAY[1..21,1..12] of REAL;
        numt:ARRAY[1..21] of REAL;
        cums:ARRAY[1..50] of REAL;
        tscore:ARRAY[1..2] of REAL;
        tz,tzero,tmax: REAL;
        rk,lmin,kk,inc,llinf:REAL;
        nlzero,ilzero,ilinf,ik,nk,nlinf,age1,age: INTEGER;
        incage,leastage,minage,maxage:INTEGER;
        id,i,l,ndist,nl:INTEGER;
        ttz,phi,a,b:REAL;
        fract,agemin,agemax,nage: REAL;
        ch:CHAR;
        fil:STRING;
        inp:TEXT;
        key:BOOLEAN;
        llzero:REAL;
        title:STRING[20];
        diffn,tbar,deltas,delt:REAL;
(**************************************************************)
BEGIN {program}
  CLRSCR;
    WRITELN('ENTER NAME OF FILE TO PROCESS');
    READLN(fil);
    ASSIGN(inp,fil);
    RESET(inp);
 WHILE NOT (EOF(inp)) DO
     BEGIN {reading from data file}
       BEGIN
         READLN(inp,lmin,nl,inc,ndist);
       END;
           FOR i:=1 TO ndist DO
            BEGIN
              READ(inp,ts[i]);
```

```
            END;
               FOR l:=1 TO nl DO {loop 810}
             BEGIN
              READ(inp,leng[l]);
               FOR i:=1 TO ndist DO
                BEGIN
                 READ(inp,num[l,i]);
                END;
             END; {810}
      LENG[NL+1]:=LENG[NL]+INC;
(*************************************************************)
  CLRSCR;
  WRITELN('SHEPHERDS LENGTH COMPOSITION ANALYSIS');
  LOWVIDEO;
  WRITE('e');
  HIGHVIDEO;
  WRITE('V');
  LOWVIDEO;
  WRITELN('alute the parameters K,Linf and t0 ?');
  ch:=READKEY;
  IF ch IN ['V','v'] THEN key := TRUE ELSE key := FALSE;
   IF key THEN
     BEGIN
         WRITELN('ENTER SPECIES NAME');
         READLN(title);
         WRITELN('ENTER VALUE FOR L-INFINITY');
         READLN(llinf);
         WRITELN('ENTER VALUE FOR K');
         READLN(kk);
         WRITELN('ENTER VALUE FOR T-ZERO');
         READLN(tz);
         WRITELN('PLEASE WAIT');
(************************************************************)
  tzero:=tz;
  rk:=1/kk;
  llzero:=llinf*(1-EXP(kk*tzero));
  FOR l:=1 TO (nl +1) DO  {loop 400}
     BEGIN
        IF leng[l] < llinf THEN key:=TRUE ELSE key:=FALSE;
           IF key THEN
            BEGIN
             tmin[l]:=rk*(LN((llinf-llzero)/(llinf-leng[l])));
            END{IF};
          END; {400}
   FOR l:=1 TO nl DO  {loop 600}
     BEGIN
      IF leng[l+1] < llinf THEN key:=TRUE ELSE key:=FALSE;
          IF key THEN
```

```
              BEGIN
               tmax:=tmin[l+1];
               delt:=tmax-tmin[l];
               tbar:=0.5*(tmax+tmin[l]);
               diffn:=SIN(PI*delt)/(PI*delt);
               cums[l]:=0.0;
            FOR id:=1 TO ndist DO  {loop 700}
             BEGIN
              discr[id]:=diffn*(COS(2*PI*(tbar-ts[id])));
              deltas:=(SQRT(num[l,id]))*discr[id];
              cums[l]:=cums[l]+deltas;
             END; {700}

        IF l >= 2 THEN key:=TRUE ELSE key:=FALSE;
            IF key THEN
              BEGIN
                 cums[l]:=cums[l]+cums[l-1];
              END{if};
         END{if};
    end{600};
(**************************************************************)
IF ch IN ['V','v'] THEN key:=TRUE ELSE key:=FALSE;
 IF key THEN
   BEGIN
    WRITELN(LST,'LENGTH COMPOSITION ANALYSIS BY SLCA FOR');
    WRITELN(LST,title);
    WRITELN(LST,' ','K=',KK:0:2,' ','Linf=',LLINF:0:2,' ','t0=',TZ:0:2);
         WRITELN(LST,'COLUMN 1 = LOWER LIMIT OF LENGTH CLASSES');
         WRITELN(LST,'COLUMN 2 = AGE');
         WRITELN(LST,'COLUMN 3 = CUMULATIVE SCORE');
             leastage:=TRUNC((tmin[1]-0.5));
             incage:=1-leastage;
                 FOR l:=1 TO nl DO {loop 900}
                   BEGIN
                    WRITELN(LST,leng[l]:10:1,tmin[L]:10:2,cums[l]:10:2);
                   END{900};
      END;
    END;
 END;
END.
```

APPENDIX [A.3]

TITLE: APE

REFERENCES: (Beamish and Fournier, 1981)

LANGUAGE: Turbo Pascal Version 5.5

HARDWARE REQUIRED: IBM compatible computer

OPERATING SYSTEM: MSDOS Version 3.3 or higher

DESCRIPTION: The program APE calculates the average percent error for a series of age determinations readings (either by the same reader or by different readers). An input file is read and the average error for each fish aged and the APE value are stored in an output file.

PROGRAM LISTING:

```
{PROGRAM WRITTEN BY ANESH GOVENDER, ORI,JAN 1991}
{This program calculates the average percent error for a}
{set of age determination readings}
PROGRAM APE;

USES CRT;

VAR av,totave,tot :REAL;               { Averages }
   ave,aves : ARRAY[1..10] OF REAL;  { Averages }
   cnt,num,i,j : INTEGER;             { Counter }
   ch : CHAR;                        { A Character }
   file_name : STRING;                { File name }
   inp : TEXT;                      { Input file }
   outt : TEXT;                     { Output File }
   x : ARRAY[1..1000,1..10] OF REAL; { Matrix of readings }
   nn : INTEGER;                   { Number of readings }

BEGIN
```

```
 CLRSCR;
 WRITELN; WRITELN;
 WRITELN('A METHOD FOR COMPARING THE PRECISION OF A SET OF AGE
DETERMINATIONS');
 WRITELN; WRITELN; WRITELN;
 WRITELN('This program was written to help fishery biologists to compare') ;
 WRITELN('the precision of age determinations. It is based on the paper of') ;
 WRITELN('R.J.Beamish and D.A.Fournier "A Method for Comparing the Precision');
 WRITELN('of a Set of Age Determinations".');
 WRITELN; WRITELN; WRITELN;
 WRITELN('this program was written by A.GOVENDER ');
 WRITELN('                    OCEANOGRAPHIC RESEARCH INSTITUTE');
 WRITELN('                    DURBAN');
 WRITELN; WRITELN; WRITELN; WRITELN;
 WRITELN('PRESS ANY KEY TO CONTINUE');
 ch := READKEY;                      { wait for input }

 CLRSCR;                { Read File name and open file }
 WRITELN; WRITELN;
 WRITELN('Enter name of file to be processed ');
 READLN(file_name);
 ASSIGN(inp,file_name);
 RESET(inp);
 WRITELN; WRITELN;         { Read Number of readings }
 WRITELN('enter the number of readings');
 READLN(nn);

 num := 0;              { Initialise number read in }
 WHILE NOT(EOF(inp)) DO
  BEGIN

   num := num + 1;            { Read another line }
   FOR j := 1 TO nn DO         { Read each line in turn }
    READ(inp,x[num,j]);
   READLN(inp);             { Skip to the next line }

  END;
 CLOSE(inp);                 { Close the input file }

 CLRSCR;
 WRITELN; WRITELN;      {output file name and create the file}
 WRITELN('Enter name of the output file');
 READLN(file_name);
 ASSIGN(outt,file_name);
 REWRITE(outt);

 FOR j := 1 TO nn DO               { Print Headings }
  WRITE(outt,'  ',j:3,'  ');
```

```
WRITELN(outt,'    APE    '); WRITELN(outt);

totave := 0;                     { initialise the variables }
FOR j := 1 TO nn DO ave[j] := 0;

FOR i := 1 TO num DO
  BEGIN

    av := 0;                       { Find the mean (X[j]) }
    FOR j := 1 TO nn DO
      av := av + X[i,j];
    av := av/nn;

    tot := 0;
    FOR j := 1 TO nn DO
      BEGIN
        if av=0 then aves[j]:=0 else {Prevent division by zero}
        aves[j] := abs(x[i,j]-av)/av;
        tot := tot + aves[j];
        ave[j] := ave[j] + aves[j];
      END;
    tot := tot/nn;
    totave := totave + tot;

    FOR j := 1 TO nn DO              { Print Output }
     WRITE(outt,'  ',x[i,j]:3:0,'  ');
    WRITELN(outt,'  ',tot:7:4,'  ');
  END;

WRITELN(outt);
FOR j := 1 TO nn DO
  WRITE(outt,' ',ave[j]/num:5:3,' ');
WRITELN(outt,'the index average error is ',totave/num:7:4);
CLOSE(outt);                       {Close the output file
```